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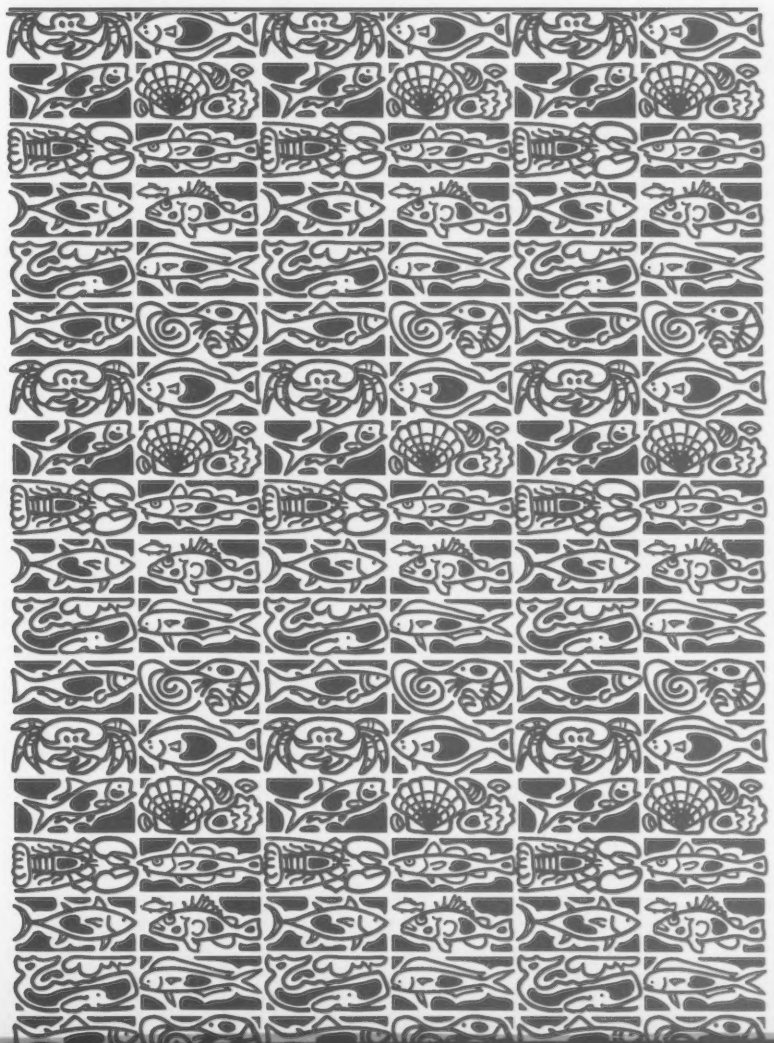

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Errata

(1)

Markle, Douglas F., Phillip M. Harris, and Christopher L. Toole

Metamorphosis and an overview of early-life-history stages in Dover sole *Microstomus pacificus*.
Fish. Bull., U.S. 90(2):285–301.

Table 4 (p. 295) should have reference to *N* (no. of trawls) deleted; the text on p. 297–298 correctly refers to Table 1 for the correct number of trawls each month.

The line art which appears in Figure 2 (p. 288) should be replaced by the following (right column):

(2)

Stone, Heath H., and Brian M. Jessop

Seasonal distribution of river herring *Alosa pseudoharengus* and *A. aestivalis* off the Atlantic coast of Nova Scotia.
Fish. Bull., U.S. 90(2):376–389.

Figure 1 (p. 377) should be corrected as follows: Depths should read 100 and 200 m, as the caption states, rather than 50 and 100 m.

(3)

Authorship of the following article should be corrected to read as follows:

Bartley, Devin, Boyd Bentley, Jon Brodziak, Richard Gomulkiewicz, Marc Mangel, and Graham A.E. Gall

Geographic variation in population genetic structure of chinook salmon from California and Oregon.
Fish. Bull., U.S. 90(1):77–100.

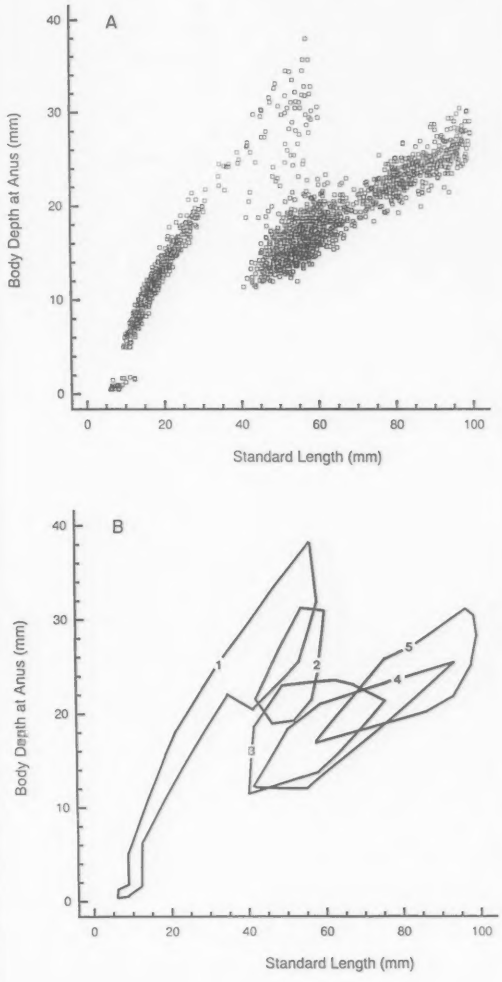

Figure 2

Relationship between body depth at anus and standard length in Dover sole *Microstomus pacificus*: (A) scatterplot of data points, Stages 1–5; (B) polygons circumscribing areas bounded by specimens in Stages 1–5.

Population characteristics of individually identified humpback whales in southeastern Alaska: Summer and fall 1986

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Abstract.– In the summer and fall of 1986 a total of 257 humpback whales *Megaptera novaeangliae* were individually identified during nonsystematic vessel surveys of southeastern Alaska. The majority of adult animals (n 130, 54.6%) identified in 1986 had been identified previously in southeastern Alaska during the years 1979–85. Capture-recapture estimates suggested that this regional subpopulation increased in abundance from 1979 to 1986, and included 547 individual whales (95% CL: 504–590) at the time of the 1986 surveys. An average reproduction rate of 0.36 calves/mature female·year^{-1} (95% CL: 0.28–0.43) was estimated for this regional subpopulation using individual identification records collected during 1980–86. In the Frederick Sound–Stephens Passage area, the largest number of whales was found during August and their predominant prey appeared to be euphausiids. In the Glacier Bay–Icy Strait area, the relative abundance of whales was greatest in June and July and their predominant prey appeared to be schooling fish. Low levels of interchange between surveyed areas for much of the summer season indicated strong preferences for local habitats among individual whales. The documented presence of some individual whales for at least 6 months is evidence that southeastern Alaska is the primary feeding ground for many of the whales identified in these surveys.

Manuscript accepted 18 May 1992.
Fishery Bulletin, U.S. 90:429–437 (1992).

Humpback whales *Megaptera novaeangliae* in the central and eastern North Pacific, like those in the western North Atlantic (Katona and Beard 1990), appear to form several geographically-isolated subpopulations during the summer and fall feeding season (Baker et al. 1986, Perry et al. 1990). Following their yearly migration south, individuals from these feeding herds intermingle in the waters of either Hawaii or Mexico during the winter breeding season (Darling and Jurasz 1983, Baker et al. 1985, Darling and McSweeney 1985, Baker et al. 1986).

The coastal waters of southeastern Alaska (56–59°N lat.) seem to encompass the primary feeding ground of a single 'herd' or regional subpopulation estimated to number between 327 and 421 individual whales as of 1983 (Baker et al. 1986). Although the exact geographic boundaries of each herd are unknown, whales from southeastern Alaska appear to remain segregated from those that summer to the west in the Gulf of Alaska, including Prince William Sound, and those which summer to the south along the coast of central California (Baker et al. 1986, Perry et al. 1990). Fidelity to a particular feeding ground appears to be maternally directed (Martin et al. 1984, Baker et al. 1987, Clapham and Mayo 1987) and may persist across many generations, as suggested by geographic segregation of mitochondrial DNA haplotypes (Baker et al. 1990).

Within southeastern Alaska, however, the distribution of whales is not homogeneous and intermingling of individuals is not random (Baker 1985a, Baker et al. 1985). Some whales return with considerable fidelity to specific areas or 'neighborhoods' such as Glacier Bay, Sitka Sound or Frederick Sound and, at least during part of the feeding season, may establish restricted local ranges (Jurasz and Palmer 1981, Perry et al. 1985, Baker et al. 1988, Straley 1990). Changes in distribution and local movement within a season appear to reflect changes in prey availability. The relatively early arrival of whales into the Glacier Bay area indicates that this may be an important area for early-summer feeding on schooling fish, including capelin *Mallotus villosus*, sand lance *Ammodytes hexapterus*, and Pacific herring *Clupea harengus* (Wing and Krieger 1983, Krieger and Wing 1984 and 1986, Perry et al. 1985).

By late summer, whales typically congregate in Frederick Sound and Stephens Passage where large swarms of euphausiids, primarily *Thysonoessa raschii* and *Euphausii pacifica*, are common (Krieger and Wing 1984, 1986). Some whales feed throughout fall and early winter in areas such as Seymour Canal and Sitka Sound where euphausiids and schooling herring appear to remain available (Baker et al. 1985, Straley 1990).

Here we summarize the results of nonsystematic surveys of individually identified humpback whales in southeastern Alaska during the summer and through late fall of 1986. The 1986 surveys were designed to overlap in geographic range and seasonal timing with previous coverage during the years 1979–85 (Baker et al. 1985, Baker 1985b). In keeping with recommended management plans (Anonymous 1984), our surveys documented regional abundance and distribution of humpback whales in areas that may be impacted directly or indirectly by vessel activity in Glacier Bay National Park. More specifically, we sought to evaluate trends in the abundance, reproductive rates, and primary prey of humpback whales in southeastern Alaska across the years 1979–86. Documentation of long-term trends in these population characteristics are valuable for assessing the influences of human activity, such as mining, logging, or petroleum exploration and development, or natural environmental fluctuations such as El Niño events, on the habitat use and recovery of this endangered species (National Marine Fisheries Service 1991).

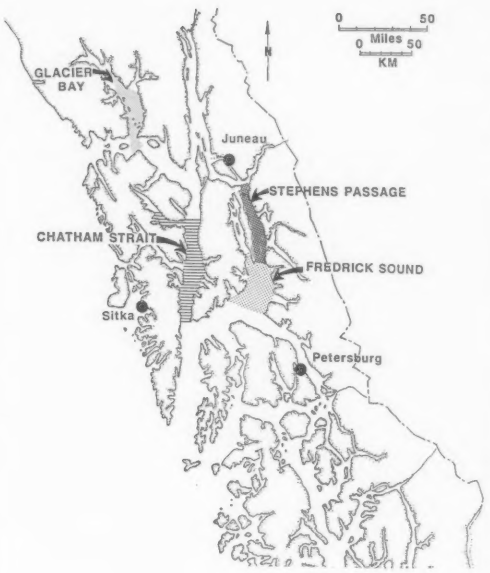

Figure 1
Southeastern Alaska region and primary survey areas (shaded).

Methods

Vessel surveys

Humpback whales were observed and individually identified primarily in two areas or subregions of southeastern Alaska (Fig. 1): Glacier Bay and the adjacent waters of Icy Strait (referred to collectively as Glacier Bay); and the contiguous waters of Stephens Passage and Frederick Sound, including Seymour Canal (referred to collectively as Frederick Sound). Photographs of whales were also collected in Chatham Strait and Sitka Sound on an opportunistic basis throughout the summer and fall.

Whales in Glacier Bay were censused by one of us (CSB) from 22 May to 10 September under the auspices of the National Park Service. A total of 42 one-day surveys were conducted aboard a 17-foot fiberglass boat powered by a 50-hp outboard motor. The lower and middle bay (i.e., from Bartlett Cove to the mouths of Muir Inlet and the West Arm) were surveyed not less than twice and not more than three times a week. The mouth of Glacier Bay and the adjacent waters of Icy Strait were surveyed at least once and not more than twice a week. Study period and survey coverage were designed to overlap and extend previous coverage during the summers of 1982–85 (Baker et al. 1985, Baker 1985b).

Whales in Frederick Sound were censused during three summer surveys: 31 July–3 August; 29 August–1 September; and 12 September–15 September. These survey cruises were conducted aboard the RV *Sashin*, a 22-foot stern-drive vessel provided by the Auke Bay Laboratory, National Marine Fisheries Service. Each cruise originated and ended in Juneau and surveyed the length of Stephens Passage and Frederick Sound south to Cape Fanshaw and west to Pybus Bay (see shaded area, Fig. 1). A fourth survey of Frederick Sound was conducted from 29 November to 9 December aboard the MV *Fairweather*, a 43-foot, diesel-powered cabin cruiser. This cruise originated and ended in Sitka, Alaska, and surveyed the southern half of Chatham Strait and Frederick Sound, north to Seymour Canal. The dates and geographic coverage of Frederick Sound surveys were chosen to coincide with those of similar previous surveys during the summers of 1984–85 (Krieger and Wing 1986, CSB unpubl. data), the fall or winters of 1979–85 (Straley 1990),

and with field efforts during the summers of 1981–82 (Baker et al. 1985).

Prey assessment

Humpback whale prey species were assessed in Glacier Bay with a Ross Fineline 250C recording fathometer equipped with a 22° beam, 105-kHz transducer. In Frederick Sound, prey were assessed with a Lowrance recording fathometer equipped with a 250-kHz transducer. Putative identification of primary prey species type (e.g., euphausiids vs. schooling fish) was based on qualitative differences in target strength, as judged from the relative intensity of fathometer recordings, and the size, shape, and depth of prey schools. These interpretations were based on reference to previous documentation of humpback whale prey using quantitative hydroacoustics and net sampling (Wing and Krieger 1983, Krieger and Wing 1984 and 1986). On occasion, observations of feces from feeding whales or the presence of prey species at the surface provided direct confirmation of primary prey species type.

Table 1

Between-years reidentification and the Petersen population estimate using Bailey's correction (in parentheses) of humpback whales *Megaptera novaeangliae* in southeastern Alaska.

Year	Identified: no. [newly]	Reidentification year						
		1980	1981	1982	1983	1984	1985	1986
1979	83	32	41	48	11	36	33	40
	[83]	(307)	(294)	(310)	(353)	(435)	(498)	(484)
1980	121	—	58	53	11	48	53	51
	[89]		(306)	(410)	(514)	(479)	(457)	(556)
1981	148	—	—	85	26	73	66	63
	[71]			(315)	(280)	(388)	(451)	(553)
1982	182	—	—	—	31	80	81	79
	[66]				(290)	(436)	(453)	(544)
1983	50	—	—	—	—	35	29	23
	[12]					(269)	(340)	(498)
1984	193	—	—	—	—	—	80	76
	[76]						(486)	(599)
1985	203	—	—	—	—	—	—	79
	[74]							(606)
1986	238	—	—	—	—	—	—	—
	[108]							
Sum	579							

Individual identification

We attempted to individually identify all humpback whales encountered by collecting photographs of the ventral surface of the whales' flukes. The uniqueness of the coloration, shape, and scarring pattern of the flukes' ventral side allowed for the reliable identification of individual whales (Katona et al. 1979). Because our primary objective was to collect individual identification photographs for use in capture-recapture analyses and the estimation of long-term reproductive rates, we did not attempt to count unidentified whales along the survey tracks. Consequently, all references to 'sightings' or 'observations' of whales are based only on photographs of unique individuals.

Methods for processing and comparison of fluke photographs followed that described by Perry et al. (1988). Photographs of whales were taken with a 35 mm single-lens reflex camera equipped with a motor drive and a 300 mm telephoto or 70–210 mm zoom lens. High-speed (ASA 400–1600) black-and-white film was used. From each observation of a whale or group of whales, the best photograph of each individual's flukes was printed and assigned a "fluke observation" or identification number. Information on the location, date, and social affiliation of each fluke identification was stored in a data retrieval file at the University of Hawaii Computing Center. During the matching of fluke photographs, a whale that was identified on more than one occasion was also assigned an "animal" number. This number allowed us to reference all fluke observations, or identifications, of that individual. All fluke photographs were judged to be of either good, fair, or poor quality. Good- and fair-quality photographs showed at least 50% of both flukes at an angle sufficiently vertical to distinguish the shape of the flukes' trailing edges. For this study, poor-quality photographs were deleted from the data set.

Results

Abundance and regional fidelity

A total of 257 humpback whales, including 19 calves, were individually identified in southeastern Alaska during 1986. This total includes 29 adults identified only in Glacier Bay, 183 identified only in Frederick Sound, 16 identified only in Sitka Sound or Chatham Strait, and 10 adults common to more than one subregion. The majority (n 130, 54.6%) of the 238 adults identified in 1986 had been identified in southeastern Alaska previously, based on comparison with photographs collected by University of Hawaii researchers and associates during the years 1979–85 (Perry et al. 1988). The addition of the 108 newly identified individuals to the existing catalogue of photographs resulted in a cumulative total of 579 adult whales identified in southeastern Alaska across the 8 study years (Table 1).

To determine the fidelity of humpback whales to regional feeding grounds, photographs collected from southeastern Alaska during 1986 were compared with

photographs of 95 individuals from the western Gulf of Alaska (von Ziegesar and Matkin 1989), 18 from central California collected during 1977–85 (Perry et al. 1988), and 225 individuals from central California identified during 1987–88 (Calambokidis et al. 1990). This comparison provided no evidence of movement by individual whales between these three feeding regions. Two whales previously identified in both southeastern Alaska and Prince William Sound (Baker et al. 1986) were not reidentified in southeastern Alaska in 1986, suggesting that their immigration to southeastern Alaska may have been temporary.

The identification and reidentification of individual animals across years lends itself to the estimation of abundance using capture-recapture formulae (e.g., Hammond 1986). Table 1 summarizes abundance estimates of the southeastern Alaska feeding herd from a pair-wise comparison of all yearly samples using the Petersen estimate with Bailey's correction (Caughley 1977). The yearly estimates range from a low of 269 (1983–84) to a high of 606 (1985–86). The weighted mean of the Petersen estimate (i.e., the Schnabel estimate; Seber 1982) across the 8-year study indicated that this regional subpopulation has included 547 animals (95% CL: 504–590).

Possible inequalities of individual reidentification probabilities were examined by calculating the identification frequencies for individual whales across the 8 study years (Table 2). The observed frequency distribution showed fewer 2- or 3-year reidentification records and more single identifications and reidentification records of extreme frequencies than expected when compared with a zero-truncated Poisson distribution calculated according to Caughley (1977). The significant departure of the observed from the expected distribution (χ^2 [4] 291, $p<0.001$) suggests that all individual whales were not equally available for reidentification during the study period. Possible causes of this unequal 'catchability' include births, deaths, and permanent emigration across the 8-year study, as well as heterogeneity of reidentification probabilities due to local habitat preferences and the limited range of surveys.

Table 2

Observed and expected frequency of yearly identifications for 579 adult humpback whales *Megaptera novaeangliae* in southeastern Alaska during the years 1979–86.

	Identification frequency (years)						
	1	2	3	4	5	6	7+
Observed	330	81	56	46	32	24	10
Expected	216	186	108	47	16	6	—

Note: Expected frequencies were calculated from the zero-truncated Poisson distribution according to the methods described by Caughley (1977).

Reproductive rates

Among the 238 adults individually identified in 1986, there were 32 cows accompanied by calves assumed to be less than a year old. Using this census information we estimated the crude birth rate in 1986 to be 0.125, calculated as the total number of identified cows (n 32) divided by the total number of identified whales of all classes (n 257, including only identified calves). This estimate, however, may have been biased by the greater visibility of cow/calf pairs and by additional effort directed towards individually identifying members of this age/sex class.

An alternate estimate of annual reproductive rates was calculated using the identification histories of individual females known to be reproductively mature prior to the 1986 surveys (Baker et al. 1987). Of the 41 mature females previously identified by Baker et al. (1987), 24 were reidentified during the 1986 surveys and 9 were accompanied by a calf, yielding an estimate of 0.375 calves/mature female·year^{-1}. The addition of the 1986 identifications provides an updated estimate of the long-term calving rates for 41 females previously discussed by Baker et al. (1987) (Table 3). Between 1980 and 1986, these 41 females were observed with 58 individual calves across 162 seasonal identifications. Although annual calving rates appeared to alternate

Table 3

Calving rates of mature female humpback whales *Megaptera novaeangliae* in southeastern Alaska, based on reproductive histories of 41 individuals identified in two or more summer seasons (see Baker et al. 1987).

	Identification year							
	1980	1981	1982	1983	1984	1985	1986	Sum
Females identified	8	33	33	12	31	21	24	162
Total calves	2	9	15	3	15	5	9*	58
Calves/female	0.25	0.27	0.45	0.25	0.48	0.24	0.38	0.36

*Includes one calf thought to have died during the summer. See text for details.

Table 4

Within-year (between-survey) reidentification and the Petersen population estimates with Bailey's correction (in parentheses) of adult humpback whales *Megaptera novaeangliae* in Glacier Bay, 1986.

Survey month	Identified: no. [newly]	No. reidentified June	July	Aug	Sept
June	27	—	17	12	7
	[27]		(42)	(39)	(37)
July	27	—	—	12	9
	[10]			(39)	(30)
August	18	—	—	—	10
	[3]				(18)
September	10	—	—	—	—
	[0]				
Sum	40				

Table 5

Within-year (between-survey) reidentification and the Petersen population estimates with Bailey's correction (in parentheses) of adult humpback whales *Megaptera novaeangliae* in Frederick Sound, 1986.

Survey dates	Identified: no. [newly]	No. reidentified 1	2	3	4
31 July–3 Aug	72	—	22	19	13
	[72]		(247)	(234)	(283)
29 Aug–1 Sept	78	—	—	23	9
	[56]			(211)	(429)
12–15 Sept	64	—	—	—	4
	[30]				(704)
29 Nov–7 Dec	54	—	—	—	—
	[36]				
Sum	194				

between high and low years from 1981 to 1986, a Test of Independence indicated that these year-to-year differences were not significant (χ^2 [6] 6.88, p 0.332). Average calving rate across the 7-year study was 0.36 calves/year (95% binomial CL: 0.284–0.432), similar to the previously reported rate of 0.37 for the years 1980–85 (Baker et al. 1987).

Local abundance and interchange

Capture-recapture estimates of seasonal abundance for the Glacier Bay and Frederick Sound subregions were calculated using the Petersen formula with Bailey's correction and treating each survey or survey period as a sample (Tables 4 and 5). In Glacier Bay, the number of individual whales identified was greatest during June and July and declined through August and September (Table 4). The percentage of newly-identified whales declined rapidly through the summer, suggesting that the census of identified individuals approached a complete count of the whales in this subregion. Capture-recapture estimates based on monthly censuses ranged from 18 to 42 and agreed closely with the total number of 40 adults identified in this subregion.

In Frederick Sound, the number of individual whales identified during each survey remained constant from late July to mid-September and declined by late fall (Table 5). The percentage of newly-identified whales decreased through the three summer surveys but increased in the late-fall survey. The Frederick Sound capture-recapture estimates from the three summer surveys ranged from 211 to 247, exceeding the total of 158 individuals identified during this period but not approaching the between-year estimates of regional abundance (see Table 1). Capture-recapture estimates increased considerably when summer surveys were compared with the fall surveys. Ranging from 283 to 704, the fall estimates agreed more closely with across-year estimates for the entire southeastern Alaska region. The larger capture-recapture estimates from the fall survey and the increase in percentage of newly identified whales suggested the dissolution of population stratification observed during the summer months or the arrival of individuals from unsurveyed areas of southeastern Alaska.

Table 6

Local movement of humpback whales *Megaptera novaeangliae* between Glacier Bay (GB) and Frederick Sound (FS) during the summer and fall of 1986.

Animal no.	From Last ident. date	To First ident. date	Interval (days)
#117	GB, 25 July	FS, 30 Aug	36
#161	GB, 22 July	FS, 2 Aug	8
#155	GB, 22 July	FS, 30 Aug	39
#196	FS, 31 July	GB, 8 Aug	8
#221	GB, 29 July	FS, 31 Aug	33
#350	GB, 21 July	FS, 30 Aug	40
#564	GB, 22 July	FS, 26 Aug	35
#566	GB, 11 July	FS, 30 Aug	50
#587	GB, 14 Aug	FS, 4 Dec	112
#616	GB, 16 July	FS, 31 July	15
#616	FS, 31 July	GB, 14 Aug	14
#616	GB, 14 Aug	FS, 30 Aug	16

Documented interchange between the southeastern Alaska subregions was limited to 12 transits by 10 individual whales (Table 6). Eight one-way transits were from Glacier Bay to Frederick Sound, and a single one-way transit was from Frederick Sound to Glacier Bay. One individual, animal #616, traveled from Glacier

Bay to Frederick Sound and back between 16 July and 14 August. Animal #616 was last identified in Frederick Sound on 30 August.

Regional occupancy

The interval between the first and last identification of an individual whale provided a minimum estimate of its occupancy in southeastern Alaska (Baker et al. 1985). Although it was not possible to document continuous residency of individual whales in either of the primary study areas (i.e., Glacier Bay or Frederick Sound), there was no evidence that individuals migrated to other known feeding regions between surveys (see 'Abundance and regional fidelity'). The longest documented regional occupancy was 192 days for animal #587. This individual was first identified on 1 June in Glacier Bay and last identified on 9 December in Frederick Sound. Animal #587's identification record, discussed by Baker et al. (1987), showed that she lost a calf sometime during the summer of 1986. Three other adults and one calf had documented occupancies of nearly equivalent length: 191 days for #616, an animal of unknown age-sex class (see also Table 6); 183 days for #350, an animal of unknown age-sex class; and 186 days for #161 and her calf.

Foraging behavior

During summer surveys, whales in Frederick Sound tended to occur in aggregations of 20 to 80 animals often clustered along submerged ridges and mounts, as determined by reference to fathometer recordings and navigational charts. Observations of whale feces and fathometer recordings of dense scattering layers below feeding whales indicated that euphausiids were the primary prey for these aggregations. During the late-fall survey, we were unable to collect fathometer recordings or to observe whale feces in order to confirm the primary prey species. However, the surface-movement and diving patterns of whales and the location of feeding aggregations were similar to that observed during summer surveys, suggesting that euphausiids were again the primary prey.

The predominant prey of humpback whales in Glacier Bay was schooling fish, as evidenced by fathometer recordings and observations of schooling fish at the surface. Within the Bay, whales fed singly or in pairs on dense schools of capelin and sandlance. Outside the Bay, in the adjacent waters of Icy Strait, the predominant prey of humpback whales appeared to be herring as demonstrated in previous years using hydroacoustic techniques and net tows (Wing and Krieger 1983, Krieger and Wing 1984 and 1986). As in previous years (Baker 1985a), whales near Icy Strait formed a socially cohesive pod of 7 to 9 individuals that appeared to cooperate in foraging on schools of herring.

Discussion

Population characteristics

The number of individual whales photographically identified during the 1986 surveys, 238 adults and 19 calves, can be considered a minimum estimate of abundance for the southeastern Alaska feeding herd. Capture-recapture analyses of across-year identification records, however, provide estimates of this regional population that are two or three times larger than that based on the 1986 census alone. Although these analyses are more likely than simple counts to provide realistic estimates of regional abundance, they should be interpreted with caution since the behavior of whales seldom conforms strictly to the theoretical assumptions underlying these models (e.g., Hammond 1986, Perry et al. 1990). Violation of the assumption of equal catchability among southeastern Alaska whales, for example, is indicated by the analysis of reidentification frequencies across the 8-year study period. Births, deaths and permanent emigration obviously contribute to this unequal catchability (i.e., reidentification inequality). Another probable source of unequal catchability is heterogeneity due to local habitat preference by individual whales and the variable and limited geographic coverage of the surveys. While births and deaths cause a positive bias in the Petersen estimate of abundance, reidentification heterogeneity causes a negative bias (Hammond 1986 and 1990).

Assuming, however, that adult mortality among humpback whales is low (e.g., Buckland 1990) and that permanent emigration to other feeding regions is infrequent (e.g., Perry et al. 1990), the weighted Petersen estimate of 547 whales (95% CL: 503–590) may be our most robust for the southeastern Alaska subpopulation in 1986. By using the cumulative reidentification records of individuals across years and weighting the final estimate by the largest sample year, the weighted Petersen should be less biased than the between-year Petersen estimates by heterogeneity due to local habitat preferences or variation in survey effort. Births during the study period are included in the cumulative population estimate when the calves mature sufficiently to become available for individual identification. The weighted Petersen is also consistent with other estimates derived from the individual identification records. The upper confidence interval of this estimate overlaps with the total count of 579 whales identified during the 8-year study and agrees closely with the unbiased Petersen estimates from the pair-

wise comparisons of years with the largest sample of identified whales, 1984–86 and 1985–86 (see Table 1).

Regardless of the exact number of individuals inhabiting this region, the individual identification surveys and mark-recapture estimates suggest that the southeastern Alaska herd increased from 1979 to 1986. In Frederick Sound, overall survey effort decreased since 1981–82 but, with the exception of 1983 when only a single 4-day survey was conducted, the number of identified whales increased. As confirmed by photographic documentation, a general increase in the number of whales in the Glacier Bay area during the last few years was the result of the continued return of past residents and the recruitment of their offspring (Baker et al. 1988). In terms of overall regional abundance, the mark-recapture estimates from pair-wise comparisons of 1986 to previous years suggest an increase from 484 to 606 across 1979–86, while estimates from contiguous years suggest an increase from 307 to 606 (Table 1). Requiring an annual rate of increase from 3.4 to 10.4%, these trends in estimated abundance are within the range reported for population growth of other unexploited baleen whales based on individual identification data (e.g., Hammond 1990, Best and Underhill 1990, Bannister 1990). More accurate estimates of the current abundance and the true rate of increase in the southeastern Alaska subpopulation will require further detailed analyses of survival rates and the biases introduced by heterogeneity of identification records.

Although apparently sufficient to sustain some degree of population growth, the observed reproduction rate of humpback whales in southeastern Alaska seemed low in comparison with other studied populations and to the maximum reproductive potential of 0.50, or even 1.00 (calves/mature female·year^{-1}) as observed in some individually identified females (Darling 1983, Glockner-Ferrari and Ferrari 1984 and 1990, Baker et al. 1987, Clapham and Mayo 1987 and 1990, Straley 1989). The estimated calving rate of 0.36 (calves/mature female·year^{-1}) across the 1980–86 study suggests that females from this region give birth to a calf that survives its first migration from the wintering grounds about once every 2.8 years. In the Gulf of Maine, Clapham and Mayo (1990) report an average reproduction rate of 0.41 (calves/mature female·year^{-1}) and an average calving interval of 2.35 years for the period 1979–87, using individual identification methods similar to those used here. Pregnancy rates from exploited populations, as summarized by Baker et al. (1987), all exceed the estimated calving rate for southeastern Alaska, although this historical comparison is confounded by differences in methodology.

Seasonal trends and foraging strategies

The number of whales identified in Glacier Bay and Icy Strait was greatest during late June and early July, and declined through August and September. Since survey effort in Glacier Bay was high relative to total number of whales identified, and constant throughout the study period, we believe that trends in the monthly censuses or counts of individuals reflected changes in seasonal abundance for this subregion. Although surveys of Frederick Sound were not frequent enough to track the seasonal increase in whales during early summer, the greatest numbers of whales were found during late July and August, approximately 1 month after the local peak in Glacier Bay.

We could not determine if these seasonal trends reflect primarily changes in the timing of migratory arrival on the feeding grounds or the pattern of local movement among subregions of southeastern Alaska. Within the geographic limits of our surveys, seasonal changes in influx were accompanied by some local movement between subregions; the decline in numbers of whales in Glacier Bay was, in part, the result of their relocation to Frederick Sound. Studies in previous years also demonstrated that local movement between these subregions tends to be one-directional, resulting in the whales congregating in Frederick Sound during late summer and fall (Baker 1984, Perry et al. 1985, Krieger and Wing 1986). Large areas of available habitat in southeastern Alaska remain entirely unsurveyed (see Fig. 1), including the outer coast of Baranof Island and the inside passage to the south of Frederick Sound. The increase in percentage of newly-identified whales during the late-fall survey of 1986 suggests local movement from these unsurveyed areas.

Local movement may be an attempt to take advantage of seasonal changes in prey availability. Humpback whales in Frederick Sound fed almost entirely on euphausiids while those in Glacier Bay fed almost entirely on schooling fish. Movement from Glacier Bay to Frederick Sound was presumably accompanied by a shift in primary prey species. Similar contrasts in the primary prey species of whales in these two subregions have been documented in previous years (Krieger and Wing 1984 and 1986). Some whales, however, showed a strong preference for particular prey species or local habitat throughout the summer. This was indicated by the persistence of certain individual whales feeding on herring in Icy Strait late through the summer, when other whales had moved to feed on euphausiids in Frederick Sound.

Stock identity and management

The summer and late-season surveys of 1986 and previous years (Baker et al. 1985) demonstrated that many whales remained to feed in southeastern Alaska for much of the summer and into late fall. Intervals between first identification and last reidentification of some individual whales indicated seasonal occupancies of at least 6 months. Since no surveys were conducted from 15 September to 29 November, it was not possible to document continuous residency of individual whales in either of the primary study areas (i.e., Glacier Bay or Frederick Sound). However, comparisons of individual identification photographs collected in the central and western Gulf of Alaska, including Prince William Sound, and along the coast of central California indicate that whales which summer in southeastern Alaska seldom migrate to alternate feeding grounds within seasons or across years (Baker et al. 1986, Perry et al. 1990). These observations are strong evidence that southeastern Alaska is the migratory terminus and primary feeding ground for a distinct herd or seasonal subpopulation of humpback whales.

Comparisons of individual identification photographs and analysis of mitochondrial DNA haplotypes demonstrate that many members of the southeastern Alaska feeding herd migrate to wintering grounds near the islands of Hawaii (Darling and Jurasz 1983, Baker et al. 1986, Perry et al. 1990, Baker et al. 1990). The migratory connection between these primary seasonal habitats provides a unique opportunity to study and protect a population of humpback whales that spends the majority of its time within U.S. coastal waters (National Marine Fisheries Service 1991).

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Precision of recruitment predictions from early life stages of marine fishes

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Abstract. – To test the hypothesis that year-class strength in marine fishes is determined in the early-larval stages, and that these stages can be used to predict recruitment, I modeled the recruitment process using a modified form of key-factor analysis. Using data compiled from the fish literature, I found a significant relationship (R^2 0.90, $P \ll 0.001$, n 97) between the mean and interannual variance of stage-specific mortality rates that provided variance estimates for the model. The R^2 values for the true correlation between abundances of small larvae and subsequent recruitment for four example species of marine fish were predicted to lie between 0.10 and 0.57, depending on the assumptions of the model. I therefore suggest that recruitment levels are fixed after the early-larval period. However, the precision of sample correlations are too low (10-yr data series) to empirically test whether abundances or mortality rates of early larvae are in reality strongly or poorly correlated with recruitment. After metamorphosis, the strength of the true relationship and the precision of sample correlations increase sufficiently to permit precise forecasting of recruitment. Recruitment is a complex process in which variation in all life stages contributes substantially to the variability in final abundance; therefore, researchers should recognize the importance of the later prerecruit stages and the interactions among all stages.

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A major problem in the management of marine fisheries is the unpredictable fluctuations in stock size resulting from variable recruitment. Hjort (1913) first recognized this recruitment variability and proposed a number of hypotheses that linked the survival of small first-feeding larvae and subsequent year-class strength (reviewed by Wooster and Bailey 1989). These hypotheses have formed the basis of much research on the early life history of fishes, research which has been largely focused on the 'critical period' during the transition from endogenous to exogenous modes of feeding. While much has been learned about the biology of larval fish, the evidence for a critical period of increased mortality and a link between the larval stage and recruitment remains equivocal (May 1974, Ware and Lambert 1985, Peterman et al. 1988, Campana et al. 1989). Explanations for this failure have ranged from sampling and technical difficulties, such as inappropriate scales of sampling (Leggett 1986, Taggart and Leggett 1987, McGurk 1989), to the suggestion that no such critical period exists, and that all prerecruit stages contribute to some degree to variability in year-class strength (Sissenwine 1984, Anderson 1988, Peterman et al. 1988).

There have been few attempts to model the recruitment process to assess the likelihood that early-larval mortality is a dominant feature of year-class variability. Manipulations of life tables have shown that small changes in larval mortality have the potential to cause great variation in recruitment (Smith 1985, Houde 1987 and 1989, Pepin and Myers 1991); however, the influence of the larval stages in a fully dynamic model incorporating variability in all stages has not been investigated. In particular, the role of postlarval mortality in causing recruitment variability is unclear and has been the cause of some controversy (Sissenwine 1984, Peterman et al. 1988, Taggart and Frank 1990, Wooster and Bailey 1989).

An often-stated justification for research on the early life history of fish is to provide short-term forecasts of recruitment, thereby allowing managers to adjust fishing regulations in response to changes in stock size (Gulland 1989). While it is obvious that the stages very close to recruitment will give the most accurate predictions, sampling these stages is often difficult and expensive (Smith 1985), unless they are caught incidentally in other fisheries. Rather, efforts have usually been concentrated on finding a predictive relationship between recruitment and the abundance or some measure of survival of larvae and recruits, on the working assumption that Hjort's hypothesis of year-class determination at this early stage is valid (Peterman et al. 1988, Cushing 1990).

The utility of short-term (i.e., annual) predictors of recruitment in the

management of fish stocks has recently been challenged by Walters and Collie (1988) and Walters (1989). In simulated management examples, Walters (1989) finds that only extremely accurate forecasts of recruitment can offer significant improvements over using the long-term mean recruitment in stock assessment models. Thus, while studies of the early stages of marine fish may reveal insights into their ecology, it is unclear whether sufficiently accurate forecasts of recruitment will ever be possible from these early stages.

In this paper I first pose the question, "How strong are the correlations between abundances or mortality rates of the early life stages and recruitment likely to be?" I develop a simple analytical model based on key-factor analysis (Varley and Gradwell 1960, Manly 1977). I use parameter estimates compiled from a literature survey to calculate the expected correlations between life stages for the prediction of fish recruitment. I suggest that the assertion that year-class strength is fixed in the early-larval stages is not general, and, furthermore, under likely field conditions it will be difficult to quantitatively test this hypothesis.

The model

I developed a simple model to simulate the variability in population numbers and the strength of correlations between life stages. In brief, the model generated annual abundances and mortality rates over a specified number of years from which correlations between early-life-history stages and recruitment were calculated. This process was repeated in a Monte Carlo fashion to estimate the sampling distribution of the correlation coefficients.

I divided the egg-recruit period into four intervals: (1) egg-yolksac larvae, (2) early-feeding larvae, (3) late-feeding larvae, and (4) juveniles from metamorphosis to age 1, which I assumed to be the age of recruitment. I assumed that populations would be sampled at five distinct times that divide the egg-recruit period into four intervals. Sampling points were: eggs spawned (N_e), first-feeding larvae (N_f), young larvae (N_l),metamorphs (N_m), and recruits (N_r). First-feeding larvae were operationally defined as larvae that have just begun to feed, while young larvae were defined as having an age of 10 days after the onset of feeding.

In any year, the number of recruits is the product of the number of eggs spawned and the survival rates of the prerecruit stages:

$$\text{Recruitment} = \text{Eggs} \cdot S_{ys} \cdot S_{el} \cdot S_{ll} \cdot S_j,$$

where the subscripts refer to the egg-yolksac, early-larval, late-larval, and juvenile periods outlined above. Expressing survival rates as instantaneous mortalities, $M = -\ln(S)$, and taking logs of the abundances give the usual equation of key-factor analysis (Varley and Gradwell 1960):

$$N_r = N_e - M_{ys} - M_{el} - M_{ll} - M_j, \quad (1)$$

where N_r and N_e are log abundances of recruits and eggs of a particular cohort, and the M_i values are interval-specific instantaneous mortalities for four intervals defined above. I assume, following Hennemuth et al. (1980) and Peterman (1981), that log abundances and instantaneous mortality rates are normally distributed with stage-specific variances described below. This multiplicative process results in lognormally distributed recruitment, consistent with empirical results (Hennemuth et al. 1980). All subsequent references to abundance made in this paper are to log-transformed values.

Since I am interested in short-term forecasting, I assumed that stock size and, therefore, mean egg production are stationary in time and that variation in egg production is independent of recruitment. Thus, in the absence of density-dependent processes, recruitment is linearly related to egg production.

To introduce stochastic variation in the model, the abundance of eggs, N_e, and the interval-specific mortality rates were simulated as normal random variables. As the time-series of egg production was stationary and my interest is in correlations rather than abundances, the abundance of eggs and the mortality rates all had a mean of 0.

To start the sequence of calculations in a given model year, the initial abundance of eggs was randomly chosen. In the simplest version of the model, which assumes mortality in each interval is independent of the others and is density-independent, the following equation was then used to calculate the numbers of each subsequent stage:

$$N_{k+1} = N_k - m_k, \quad (1)$$

where N_k is the abundance of stage k, and m is a normal random deviate that simulates random interannual variability in mortality of interval k.

The complete independence of mortality of one stage with that of a subsequent stage is probably an unrealistic assumption because, for example, years which are good for yolksac larval survival may also be good for the survival of older larvae. This can be modeled by introducing covariances between the interval-specific mortality rates (Gerrodette et al. 1984). Covariation between interval-specific mortality rates was modeled by assuming that there was a positive corre-

lation between the mortality rate of adjacent intervals across years. The mortality of a given interval in any model year then depends partially on the mortality of the previous period in that same year. With ρ equal to the correlation between adjacent interval-specific mortality rates, I used the following equation to calculate the mortality rate of successive intervals:

$$M_{k+1} = \rho \left\{ \frac{SD(M_{k+1})}{SD(M_k)} \right\} M_k + (1 - \rho^2)^{1/2} M_{k+1}.$$

In this equation, the actual mortality for stage k+1 is a linear combination of the random variables simulating the variability in stages k and k+1. The correlation coefficient determines how much mortality in stage k+1 is similar to that of stage k. The ratio of standard deviations in the first term scales the contribution of the mortality of the previous interval to the appropriate variance. To simplify, I assumed throughout this paper that there was no covariance between the number of eggs spawned and mortality in subsequent intervals.

Finally, density-dependent mortality was incorporated in some versions of the model. Density-dependent mortality was added to the juvenile period, following suggestions of Houde (1987) and Smith (1985) that this is the most likely interval for density effects. While a number of formulations are possible, I chose a power function (Peterman 1982):

$$Y = aX^b,$$

where in this case X and Y are the abundances of juveniles and recruits, respectively. For density-independent mortality, b = 1; b is <1 for density-dependent cases. The parameter a is thus the density-independent survival rate. After taking logs, the log of the abundance of recruits is now a function of the log of the number of metamorphs, N_m, and the density-independent mortality, M_j:

$$N_r = bN_m - M_j. \quad (2)$$

In the stochastic simulations, this equation was used to calculate recruitment with a random normal deviate substituted for M_j.

The full model was run for 1000 10-yr trials in SAS (1987), and a matrix of abundances and mortality rates for each stage was built up. For each 10-yr trial, correlation coefficients were calculated between the various predictors of recruitment (i.e., abundances and mortality rates of each of the prerecruit stages), and the numbers of recruits and summary statistics of the distributions of correlation coefficients were derived.

Table 1

Daily mortality rates (M) and interval durations (t, in days) for four species used as examples in the analysis. Egg mortality includes the yolksac period up to first feeding; larval periods explained in text. Values were adapted from Houde (1987; cod *Gadus morhua*, and herring *Clupea harengus*), Smith (1985; anchovy *Engraulis mordax*), and Zijlstra and Witte (1985; plaice *Pleuronectes platessa*).

	Egg		Early larvae		Late larvae		Juveniles	
Species	M	t	M	t	M	t	M	t
Cod	0.061	18	0.160	10	0.063	46	0.010	291
Herring	0.050	21	0.080	10	0.034	70	0.015	264
Anchovy	0.250	7	0.160	10	0.050	79	0.012	269
Plaice	0.068	38	0.104	10	0.045	77	0.008	245

Model parameters

To generalize the results, I used four fish species as examples (Table 1). These were not chosen to be representative of a specific stock or situation, but rather to indicate the effect of different life histories on our ability to forecast recruitment. To parameterize the model for a specific species, the interannual variance of the number of eggs laid and the mortality of each prerecruit stage was required.

I obtained estimates of the variance in the number of eggs spawned from published reconstructions of stock abundances (Table 2). Except for cod, I used the residuals of linear regressions of log(eggs) on time to estimate the variance, since time trends existed for some stocks.

Estimates of the variability in mortality rates for all prerecruit stages are unavailable; I therefore sought a predictive relationship between interannual variance and the mean of daily mortality rates. This allowed estimation of the variances of mortality rates of the early life stages from mean daily rates. I surveyed the literature for papers containing 2 or more years of estimates of age- or stage-specific mortality for the same population or stock. All stages from egg to adult were used, for marine, freshwater, and anadramous fish species. No screening of the data was done except for estimates from adult fish, where only estimates using methods independent of catch-data analysis were used (i.e., tagging). Most adult estimates were from lightly or unfished stocks. In some cases I estimated mortality from annual estimates of abundance or from regressions of log abundance on time. All estimates were converted to daily values using annual estimates of stage duration if available, or the long-term average stage duration. Daily mortalities were then averaged

over the number of years of data available, and the variance calculated. Both variates were log-transformed, and a least-squares regression was fitted to the data.

I used the variance-mean relationship to calculate the interannual variance in mortality from mean daily mortality rates extracted from published life tables (Table 1). I split the larval period and defined the first 10 days of feeding as the early stage. This period corresponds to the usual definition of the 'critical period' for first-feeding larvae (Leggett 1986): few marine larvae can survive more than 10 days without feeding (Miller et al. 1988). Except for anchovy, where values were taken directly from Smith (1985), the daily mortality rate for the early period was set at twice the average rate for the whole larval period. Mortality rates for the late period were adjusted so that the mortality for the total larval period matched the published life tables. The result of these calculations was that the daily mortality rates of the early-larval interval were about 2.5 times those for the late-larval period. It is difficult to assess whether this decline is realistic, because there is considerable variability in the decline in mortality over time in empirical studies; in many cases mortality has been found to be nearly constant over much of the larval period (Dahlberg 1979), while there are other cases where significant declines have been observed (i.e., Savoy and Crecco 1988). Declines in mortality with larval age may be accentuated by a possible bias due to sampling interval (Taggart and Frank 1990). The variance in mortality over the duration of a particular interval was then calculated as the product of the square of the interval's duration (in days), and the variance of the daily mortality rate predicted from the variance-mean relationship.

Covariation in mortality rates

Two scenarios were developed concerning the effects of covariation between mortality rates. In the independent case, all mortality rates were varied independently of one another, while for the 'covariance' version, mortality rates of adjacent stages were assumed to be correlated across years. Few data are available to estimate the strength of these correlations, so I assumed ρ values for the correlations between adjacent M_k based on the likelihood of common agents of mortality. I assigned a relatively low ρ value of 0.25 for the correlation between the egg/yolksac period and the early-larval mortality because early-larval mortality is thought to be strongly affected by feeding success, which does not affect egg survival. Nonetheless, predation pressures are probably similar for both stages, causing some covariation in mortality rates. A ρ value of 0.5 was used between the early- and late-larval intervals because of the similarity of habitat between these two periods. For the pelagic species, anchovy and herring, $\rho = 0.25$ was used for the correlation between the late-larval and juvenile intervals, while for the demersal species, cod and plaice, I set $\rho = 0$, reflecting the major habitat shifts associated with metamorphosis.

Table 2

Interannual variability in log-transformed egg production and recruitment, compiled from literature values. All egg estimates are residuals from linear regressions of log abundance on time, except for cod where an intermediate value between herring and plaice was used.

Species	$Var(N_e)$	$Var(N_r)$
Cod	0.075	0.40
Herring	0.081	1.92
Anchovy	0.282	1.91
Plaice	0.055	0.14

Data sources
Cod: mean of 5 northwest Atlantic stocks in Koslow et al. (1987).
Herring: mean of 7 northwest Atlantic stocks in Winters and Wheeler (1987).
Anchovy: eggs—Peterman et al. (1988), recruitment—Methot (1989).
Plaice: Bannister (1978).

Density-dependence

To explore the effects of density-dependence on correlations, I ran the model with $b = 1.0$, the density-independent case, or $b = 0.7$, simulating moderately strong density-dependent mortality. The variance of juvenile mortality predicted from Figure 1 is in fact the sum of both the density-independent and density-dependent sources of mortality. To estimate the density-independent component of mortality (M_j) required for Eq. (2), I had to remove the density-dependent mortality from the total juvenile mortality predicted by Figure 1. Rearranging Eq. (2) and solving for the total juvenile mortality (M_{jtot}) yields

$$M_{jtot} = N_m - N_r = (1 - b)N_m + M_j.$$

In the models without covariances between mortality rates, and in the covariance model for cod and plaice where there is no covariation in mortality across metamorphosis, taking variances yields

$$Var(M_j) = Var(M_{jtot}) - (1 - b)^2 Var(N_m).$$

In these cases, to find $Var(M_j)$ I ran the stochastic

model up to the metamorph stage and calculated the median $Var(N_m)$. $Var(M_j)$ was then found by subtraction using $Var(M_{jtot})$ predicted from Figure 1 (Table 3). For herring and anchovy in the covariance model, the equation above should include a term for the covariance between M_{jtot} and N_m. In these cases, $Var(M_j)$ was found by trial by running the model with different values of $Var(M_j)$ and matching the median M_{jtot} with the value predicted from the regression equation of Figure 1.

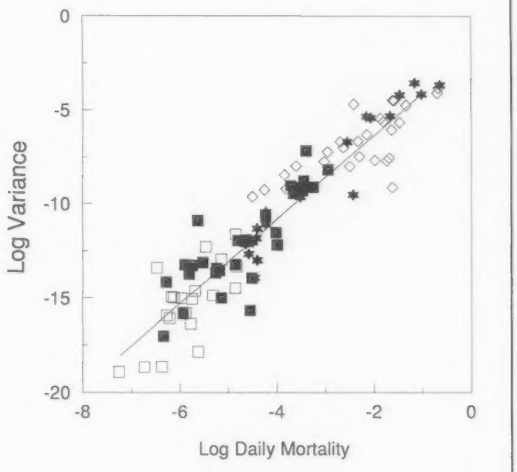

Figure 1

Relationship between interannual variance in daily mortality rates and mean daily mortality from published values. Symbols indicate eggs (*), larvae (◇), juveniles (■), and adults (□). Equation of the line: $\ln\{Var(M)\} = 2.231 \ln(M) - 1.893$ (R^2 0.90, $P<0.0001$). Regression uses the square root of number of years comprising each data point as weights.

Table 3

Variances of juvenile mortality rates $V(M_j)$ used in the four versions of the model and the variance of log recruitment, $V(N_r)$, generated by the model. Model versions include density-dependent (DD) or independent (DI) juvenile mortality and, in some cases, covariance between stage-specific mortality rates (COV). Variances for M_j in the DD models are for the density-independent component only, and were found by simulation.

	DI		DI-COV		DD		DD-COV	
Species	$V(M_j)$	$V(N_r)$	$V(M_j)$	$V(N_r)$	$V(M_j)$	$V(N_r)$	$V(M_j)$	$V(N_r)$
Cod	0.45	1.49	0.45	2.04	0.35	0.87	0.34	1.15
Herring	0.91	1.49	0.91	2.08	0.85	1.14	0.92	1.59
Anchovy	0.58	2.54	0.58	3.91	0.40	1.36	0.45	2.16
Plaice	0.22	1.64	0.22	2.46	0.09	0.79	0.09	1.04

To provide objective criteria for evaluating recruitment hypotheses, I defined two performance criteria for the correlations with recruitment. Recruitment research is commonly cast as a search for the stage when "year-class strength is determined" or "recruitment is fixed." I define such a stage as having an $R^2>0.50$ with recruitment, i.e., being able to account for at least half of the variability in year-class strength. A more rigorous standard of $R^2>0.80$ was set for correlations to be used for management purposes (Walters 1989).

Results

Variance-mean relationship

There was a highly significant relationship (R^2 0.90, $P<0.0001$, n 97) between the log of mean daily stage-specific mortality and the log of the interannual variance in the daily mortality rate (Fig. 1). The variance in mortality rate was independent of the number of years of data comprising each point (multiple regression with mean mortality, P 0.81 for sample size). The square root of sample size was used as a weight in all analyses. There was no significant effect of life history (freshwater, marine, or anadramous) on the variance-mean relationship (ANCOVAR; for slopes and adjusted means, all $P>0.20$). There was no difference in the relationship between the variance and mean of mortality among the egg, juvenile, and adult stages ($P>0.5$), but the slope for the larval stage was significantly different from the other three stages (intercept P 0.10, slope P 0.010). Because there were a number of studies on the same species, I also averaged the data across both species and stage to decrease the non-independence of the data due to common phylogeny. The variance-mean regression for this averaged dataset was almost identical to the full set (R^2 0.92, $P<0.0001$, n 53); the regression parameters differed by <2%. In this case, the regression for the larvae was not different than for the other three stages (intercept P 0.28, slope P 0.11), suggesting the significant effect found for the full dataset may have been due to the overrepresentation of some species. I therefore used the overall regression (Fig. 1) to predict the variance of mortality of all stages, rather than using a separate regression for larvae. This is a conservative procedure for rejecting Hjort's hypothesis, because the single regression predicts a more variable mortality for the early-larval stage than does the separate larval regression; the single regression produces stronger correlations between abundance of

early larvae and recruitment than the separate larval regression.

Correlations between early life history and recruitment

Correlations between abundances at early life stages and recruitment increased in strength as the interval between the two stages decreased (Figs. 2, 3). Overall, covariances in mortality rates across stages increased R^2 values between early abundances and recruitment by 0.01–0.25, while density-dependent juvenile mortality had only a small and usually negative effect on R^2 values.

Correlations between egg or first-feeding larvae and recruitment were weak; the average R^2 over all species and models was 0.05 for eggs and 0.20 for first-feeding larvae. None of the values exceeded 0.50, indicating that these early stages have little predictive capability. At the end of the early-larval stage, R^2 values increased; and in 4 of 16 cases in Figures 2 and 3 the R^2 values exceeded 0.50. However, no values exceeded 0.80, the suggested requirement for recruitment forecasting to be beneficial for management (Walters 1989).

In nearly all cases, the majority ($R^2>0.50$) of recruitment variation was predictable at the age of metamorphosis. The exception was the herring example, which gave low correlations because of high variability in the juvenile mortality rate. Half the correlations met the forecasting requirement of $R^2>0.80$ by the age of metamorphosis; these cases occurred in species with the lowest juvenile mortality rates.

The success of larval mortality rates in predicting recruitment was lower than for larval abundance estimates. The correlation between the mortality rate of the early-larval period and recruitment was strongly affected by the presence of covariation between stage-specific mortality rates; without these covariances the average R^2 was 0.12; the largest value was 0.18. When the covariances were incorporated, these correlations are increased, although none exceed 0.5 (Fig. 4). Ten of 16 R^2 values exceeded 0.50 for the much

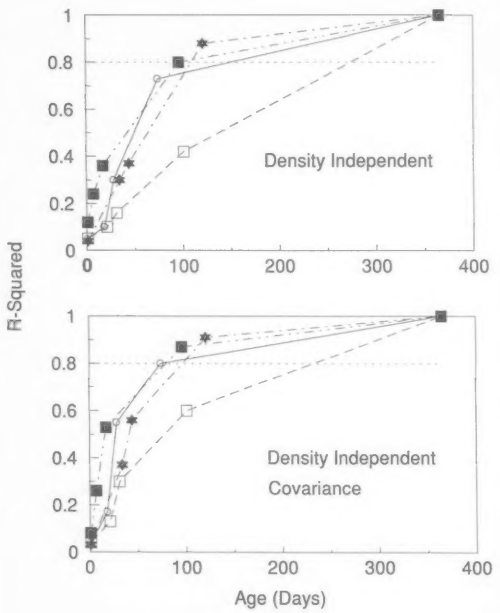

Figure 2

Predicted R^2 values for correlations between recruitment and early life stages for cod (○), anchovy (■), plaice (*), and herring (□). For each species, symbols represent, from left to right: abundance of eggs (at t = 0), first-feeding larvae, 10-d larvae, and metamorphs. Dotted line indicates the strength of correlations required for recruitment prediction (Walters 1989). Both examples include density-independent juvenile mortality; lower panel also incorporates covariance between interval-specific mortality rates.

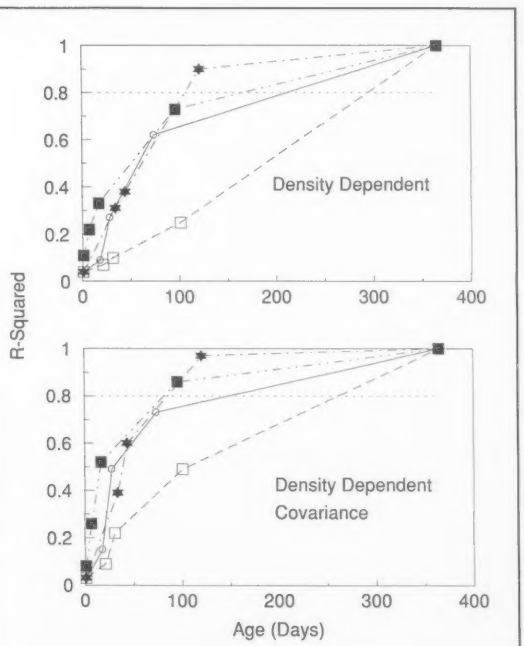

Figure 3

As in Figure 2, except both versions include density-dependent juvenile mortality; lower panel also incorporates mortality covariances.

longer late-larval period. The recruitment-forecasting threshold of 0.8 was never reached for correlations between recruitment and any larval mortality rate.

A wide range of R^2 values can result from a short time-series. For example, the 95% range of R^2 values for the correlation of early cod larvae with recruitment (10-yr time-series) in the density-independent model that includes covariance in mortality rates extended from 0.07 to 0.86 (Fig. 5). The 95% range decreases if the true relationship between the variables is stronger; for cod metamorphs the conclusion that this stage can be used to describe the majority of recruitment variation will nearly always be reached (Fig. 5).

Sensitivity analysis

Two sensitivity analyses were conducted to assess dependence of the results on input parameters. First, stage-specific variances in mortality were recalculated with the slope of the variance-mean regression set at its 95% confidence limits; the intercept was derived by constraining the line through the mean of both variables. For the cod-DI model, increasing the slope to the upper confidence limit increased the R^2 for the correlations between the abundance of recruits and early larvae or metamorphs by about 0.05; decreasing the slope lowered R^2 values by similar amounts. There was little effect on correlations involving the egg or first-feeding stages. I also recalculated the correlations with the intercept of the variance-mean regression at its 95% confidence limits. With the intercept at its lower limit, R^2 values increased by 0.01–0.04, and at the upper limit the correlations decreased by a similar amount. Thus, the overall results are not particularly sensitive to the sampling error associated with the data in Figure 1.

I also varied the length of the early-larval period. In the life tables (Table 2), I fixed the early-larval period at 10 days and set the daily mortality rate at twice the average for the whole larval period. In sensitivity runs I varied this period from 5 to 15 days; duration and mortality rate of the late-larval period were recalculated to keep the total mortality for the larval period constant. The duration of this period of high larval mortality had a strong effect on the strength of the correlation between abundance of larvae sampled at the end of the early period and recruitment. When the early-larval period was increased by 5 days, the R^2 in the cod-DI model increased by 0.21 (Fig. 6).

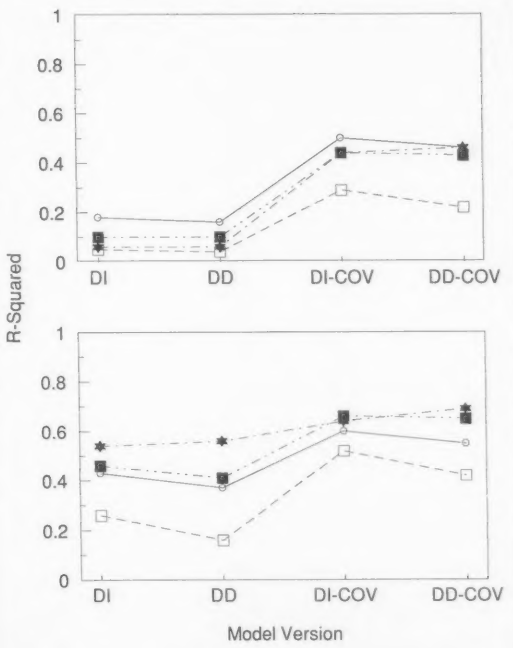

Figure 4

Predicted R^2 values for correlations between recruitment and early- and late-larval mortality rates for cod (O), anchovy (■), plaice (•), and herring (□). Axis labels refer to four versions of the model, incorporating density-independent (DI) or -dependent (DD) juvenile mortality and covariances between mortalities (COV).

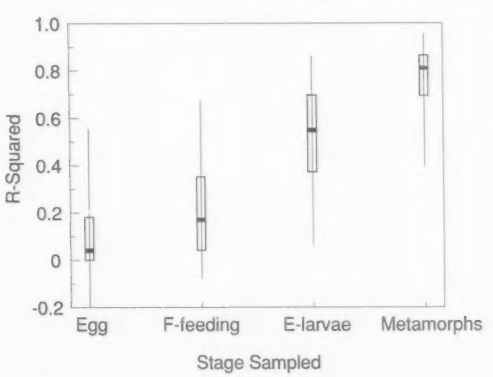

Figure 5

Variability in sample R^2 values (10-yr series) for the correlation between recruitment and abundances of early stages for cod in the model, with density-independent juvenile mortality and mortality covariances. Shown are the median (bar), interquartile (rectangle), and 95% ranges (line). Data are from 1000 runs; note that the criterion for significance ($R^2>0$, α 0.05) is 0.40.

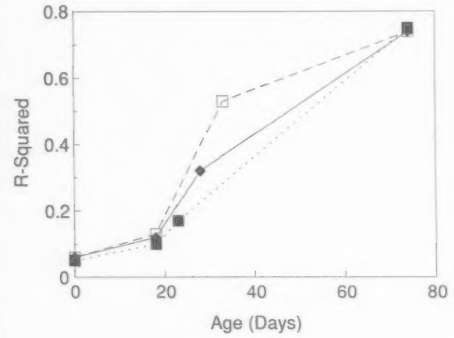

Figure 6

Effects of altering length of the early-larval stage on recruitment correlation for the cod DI-COV model. Early stage is defined as having twice the daily mortality rate of the total larval period. Shown are results with the early stage set at 5 (■), 10 (◆), and 15 (□) days. Symbols represent, from left to right: egg, yolk-sac larvae, early larvae, and metamorph stages.

Discussion

My results indicate that only predictions of recruitment based on abundances of postmetamorphic fish are likely to be useful for the management of marine fishes. The contribution to recruitment variation made by egg number (and, therefore, stock biomass) is very small, a prediction confirmed by most stock-recruit data (Parrish 1973). Correlations involving the abundance of early larvae are stronger, but are still too weak for forecasting. The model R^2 values for correlations involving early larvae are similar to the range, extending from 0.01 to 0.66, for published values compiled by Peterman et al. (1988). Accurate recruitment forecasting may be possible by sampling during the late-larval period (Graham and Sherman 1987). However, this is highly dependent on parameters and the dynamics of the particular species; only for cases with low variability in juvenile mortality or with mortality rates correlated across stages are the abundances of late larvae likely to be useful for recruitment forecasting.

Research on recruitment variability has been oriented to the early-larval stages largely as the result of Hjort's (1913) hypotheses and the observation that most of the individuals of a year-class die during the first few weeks of life (Wooster and Bailey 1989). In my four example species, the average cumulative mortality on the cohort to the 10-d larval stage is 93% (Table 1), yet the variation in abundance of these larvae explains more than 50% of recruitment variability in less than half of the cases. Variability in the late-larval and juvenile stages is still large enough to influence the strength of correlations of recruitment with larval abundances. My results suggest that the stage 'when year-class strength is determined' (defined here as $R^2>0.5$) occurs after this early critical period. However, the sensitivity analysis indicates that the strength of the correlation between the abundance of larvae and recruitment will depend strongly on the rate at which mortality declines during the larval period, and at what age the larvae are being sampled.

Strong linkages in mortality rates across intervals also render the definition of a 'critical period' less concise. Correlations between early life stages and recruitment were stronger when there were linkages, because survival to the age of sampling will be correlated to survival in the future. An estimate of mortality or abundance in one stage will be an index of mortality in all early life stages. This may be especially true for the early-larval stages (the classical 'critical period') because small larvae are probably subjected to a similar source of mortality as older larvae, especially if spawning occurs over a protracted period, mixing larvae of different ages together in the same body of water. In addition, environmental conditions during an early stage may affect survival of the cohort in the future. Poor feeding conditions of early larvae, for example, may have a long-term effect on growth and survival (Frank and McRuer 1989). In these cases, recruitment will be somewhat predictable from the early-larval stages, but this is not support for a strict interpretation of Hjort's hypothesis that an early critical period determines recruitment because mortality is correlated across all prerecruit stages.

The difficulty and expense of obtaining accurate estimates of abundances of eggs and larval fish have led to increased interest in finding indirect estimates of mortality rates that may be simpler to collect and could provide an index of year-class strength. Such measures include estimates of growth (Houde 1987), condition, lipid content (Theilacker 1986), and RNA/DNA ratios (Buckley and Lough 1987) as well as oceanographic variables such as upwelling and wind events (Peterman and Bradford 1987). My results show that such mortality estimates made on small larvae are not likely to be strongly correlated with recruitment (Fig. 4). Mortality estimates on older larvae will have stronger correlations, potentially closer to a value of 0.50. Note that the correlations in Figure 4 are for direct estimates of mortality, indirect indices will be more poorly related to recruitment. A combination of larval abundances and mortality rate estimates may allow more precise prediction of recruitment (Graham and Sherman 1987, Frank and McRuer 1989); if estimates are accurate and are based on older larvae,

correlations nearly as strong as those predicted for metamorphs might be possible.

The correlations will be weaker if sampling errors are included in the estimates of abundance. Preliminary simulations with random sampling errors with a coefficient of variation of 50% (untransformed abundances) decreased R^2 values in Figures 2 and 3 by 0.10–0.15 (Bradford unpubl.). Biased estimates, e.g., due to gear avoidance (Lo et al. 1989), will not affect correlations between an early stage and recruitment, unless the magnitude of the bias is correlated with the estimate. Precision, through the use of consistent technique across years, is more important for the purposes of forecasting. Large-scale surveys of abundance of late larvae or juveniles may be sufficiently accurate for the forecasting of recruitment (Lo et al. 1989) if the stage sampled is likely to be strongly correlated with recruitment (Fig. 5).

An implicit, though infrequently stated, assumption of research on early-life-history influences on recruitment is that the mean and the interannual variance of mortality rates are correlated. High mortality alone will not cause recruitment variation; it must also be coupled with high interannual variability. The data compiled in Figure 1 provide evidence that this is generally true, and that the interannual variability in the larval period is proportionately no greater than that found for other stages. In addition, my sensitivity analysis suggests that the general conclusions of this paper are robust to the sampling variability of this relationship. However, detailed investigation of the recruitment dynamics of an individual species will require estimation of the variance of stage-specific mortality rates, because the predictive power of Figure 1 is still relatively low for any particular case, and the biology of an individual species may not result in rates that follow the overall average pattern. Examples are provided by species which spawn during periods of extreme climatic events such as wind storms (e.g., capelin *Mallotus villosus* or red drum *Sciaenops ocellatus*, reviewed by Taggart and Frank 1990). In these cases, interannual variability in the mortality of the earliest stages is probably larger than predicted by the regression of Figure 1, and the correlation between the early stages and recruitment is likely to be stronger than I have predicted. In contrast, for the North Sea plaice a relationship (R^2 0.7) was found between egg abundance and recruitment (Zijlstra and Witte 1985), which is higher than my model predicts for this species (although just within the 95% range). This species has relatively low recruitment variation, suggesting that larval and juvenile survival rates are not as variable as predicted by Figure 1, or that density-dependent mortality might be important in regulating recruitment (Zijlstra and Witte 1985).

The recruitment variances generated by various versions of the model tend to be higher than published values (Tables 2, 3). These literature estimates will likely be underestimates of the true variability in recruitment, because errors in catch sampling and ageing can greatly reduce recruitment variability estimated from sequential population analysis (Rivard 1989, Bradford 1991). Alternatively, my recruitment variances could be too high because I have either overestimated the variances of mortality rates or underestimated the severity of density-dependent mortality. Since the data in Figure 1 include sampling error, all of the variances in Tables 2 and 3 will be somewhat inflated. If sampling error is proportional to the rate of mortality, the sensitivity analysis suggests that removing sampling error (i.e., lowering the intercept of Fig. 1) will have only a slight effect on recruitment correlations.

One additional source of variability not explicitly considered in my analysis is the effect of varying stage duration, due to interannual variability in growth rates. Houde (1987, 1989) has demonstrated through life-table manipulation that small variations in larval growth may have large effects on the number of metamorphs produced. The effect on recruitment will be buffered somewhat as shortening the larval period will increase the length and, therefore, the total mortality of the juvenile stage. However, if the variation in growth rates is due to temperature, Pepin (1991) suggests that the offsetting effects of temperature on development and mortality will result in no net effect of temperature variation on cumulative mortality over the egg and larval stages. In this case, by not including variation in growth rates I will have overestimated the variability in larval mortality. However, to some extent the effects of growth-rate variation are already included in my model because many of the estimates in Figure 1 are based on total stage length and will, therefore, include the effects of varying stage duration caused by variation in growth rates in the calculation of the average daily mortality rate.

The sampling variability of correlations from short datasets makes it difficult to draw inferences about the causes of recruitment variability. This low precision suggests that confidence limits around the sample estimates, r or R^2, should always be supplied, much in the same way that standard errors are given for sample means. A population correlation from Figures 2 and 3 is a value that would be obtained from a very long time-series of data, and is a true measure (in the context of the model) of the contribution of an early life stage to recruitment variation. However, there is a good chance (e.g., >30% for early larvae in Fig. 5) that a sample correlation between the abundance of an early stage and recruitment may not be significantly different from 0. Even if the correlation is significant,

statements about whether the relationship is, in reality, weak or strong cannot be made because the 95% confidence limits around the sample correlation are wide (Fig. 5). Published correlations between early life stages and recruitment vary greatly in strength (e.g., Peterman et al. 1988, Stevenson et al. 1989, Cushing 1990); unfortunately with short data series, true differences in the biology of these species cannot be distinguished from sampling error. The correlations between early larval abundances and recruitment compiled by Peterman et al. (1988) also illustrate this point: in only 1 of 7 cases do the 95% confidence limits around R^2 not include both 0.2 and 0.8. This problem of low precision is less serious when the true correlation is likely to be fairly high (Fig. 5, metamorphs).

The precision of correlations is also relevant to analyses involving oceanographic or climatic variables and recruitment. These studies usually invoke hypotheses that the environmental variables are agents of larval mortality, either through transport or their effects on the production or concentration of larval food (Shepherd et al. 1984, Hollowed and Bailey 1989); therefore, their true correlations with recruitment can be no stronger than the correlations for mortality rates directly (Fig. 4). Yet the sampling variability of R^2 for a short series of data suggests that there will be a good chance of finding at least one strong sample correlation among a group of 4–5 predictors that may be, in reality, only weakly related to recruitment. Adding more data will result in the sample correlation declining towards ρ; this frequently results in the sample correlation becoming nonsignificant (Koslow et al. 1987, Walters and Collie 1988, Prager and Hoenig 1989). My model results suggest environmental variables will be strongly correlated with recruitment only if the environmental factor is related to mortality across all prerecruit stages (e.g., Fig. 4; covariance models).

In summary, my analysis indicates that it is unlikely that estimates of abundance of survival rates of the egg and early-larval stages of marine fish will lead to useful predictions of recruitment. Although mortality in the earliest life stages is a major source of recruitment variability, the late-larval and juvenile periods are also important. Peterman et al. (1988), Fritz et al. (1990), and Pepin and Myers (1991) argue for the need for coordinated research on all prerecruit stages, rather than focusing only on the early stages, and my results support this view. The modeling approach I have developed here can be easily modified for any particular species to estimate *a priori* the likelihood of success of proposed recruitment research and to suggest particularly fruitful avenues of investigation.

Acknowledgments

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Appendix

Daily mortality rates and interannual variances plotted in Figure 1. Stage refers to egg (E), larval (L), juvenile (J), or adult (A) periods. For anadromous salmon, fry-smolt and smolt-adult mortality were classified as juvenile and adult mortality, respectively. *N* is the number of years of data in each study.

Species	Stage	M	var(M)	*N*	Study
Alosa pseudoharengus	L	0.0490	4.31E-04	9	Mansfield and Jude 1986
	L	0.1980	1.07E-04	8	Walton 1987
A. sapidissima	L	0.0524	2.96E-04	8	Savoy and Crecco 1988
	L	0.0978	1.28E-03	8	
	L	0.2290	3.50E-03	8	
	J	0.0027	1.30E-07	8	
	J	0.0185	5.08E-06	8	
Clupea harengus	E	0.3135	2.80E-02	2	Dragesund and Nakken 1973
	L	0.2060	1.10E-02	2	
	L	0.0275	3.38E-04	11	Graham and Sherman 1987
	L	0.1168	1.83E-03	4	Johannessen 1986
	L	0.0900	8.98E-03	2	McGurk 1989
Cololabis saira	L	0.0726	9.19E-04	14	Watanabe and Lo 1989
Coregonus artedii	L	0.5000	1.63E-02	2	Hatch and Underhill 1988
C. clupeaformis	E	0.0299	6.40E-05	2	Taylor et al. 1987
	L	0.0143	9.30E-05	2	
	L	0.0216	2.10E-04	2	Freeberg et al. 1990
Engraulis encrasicolis	L	0.2000	1.11E-02	3	Palomera and Lleonart 1989
E. mordax	E	0.3600	1.53E-02	13	Peterman et al. 1988
	L	0.1860	5.52E-04	13	
	J	0.0180	9.77E-06	13	
Esox lucius	L	0.1650	3.60E-03	3	Franklin and Smith 1963
Gadus morhua	E	0.1890	4.84E-03	3	Campana et al. 1989
	L	0.1940	2.37E-03	3	
	E	0.2304	1.48E-02	7	Heessen and Rijnsdorp 1989
	L	0.1010	5.63E-04	8	Sunby et al. 1989
	J	0.0312	8.90E-05	7	
Melanogrammus aeglefinus	E	0.1270	4.43E-03	3	Campana et al. 1989
	L	0.2630	8.56E-03	3	
Micropterous dolomieui	E	0.0890	7.12E-05	3	Clady 1975
	L	0.0310	7.74E-05	3	
	A	0.0007	6.00E-09	2	Van Woert 1980
M. salmoides	L	0.0224	9.90E-05	3	Kramer and Smith 1962
	J	0.0078	1.80E-06	4	
Morone saxatilis	L	0.1770	4.50E-04	2	Dey 1981
	J	0.0040	2.00E-06	2	
	L	0.1550	4.30E-03	6	Uphoff 1989
	J	0.0530	2.80E-04	10	Turner and Chadwick 1972
Oncorhynchus gorbuscha	E	0.0097	5.32E-06	6	Pritchard 1948
	J	0.0260	7.80E-05	3	Parker 1968
	A	0.0080	1.65E-06	3	
O. kisutch	A	0.0028	1.37E-07	8	Mathews 1984
	A	0.0078	5.15E-07	17	Mathews and Olson 1980
	A	0.0049	3.51E-07	22	Nickelson 1986
O. mykiss	J	0.0036	1.85E-05	3	Seelbach 1987
	A	0.0020	1.02E-07	4	Allen 1977
	A	0.0022	3.08E-07	7	Ward and Slaney 1988

Appendix (continued)

Species	Stage	M	var(M)	*N*	Study
Oncorhynchus nerka					
Sixmile Creek	E	0.0103	3.15E-06	2	Foerster 1968
Scully Creek	E	0.0116	8.82E-07	6	
Williams Creek	E	0.0111	5.91E-06	3	
Chilko Creek	E	0.0123	2.24E-06	7	
Tally Creek	E	0.0146	1.53E-05	11	
Port John Lake	E	0.0123	1.20E-05	9	
Karymai Spring	E	0.0120	7.23E-06	8	
Chilko Lake	J	0.0018	3.96E-08	7	
Karymai Spring	J	0.0056	1.31E-06	8	
Cultus Lake	J	0.0053	1.47E-06	10	
Port John Lake	J	0.0028	1.77E-06	8	
Babine Lake	J	0.0052	1.17E-06	10	
	J	0.0032	1.72E-06	14	McDonald and Hume 1984
	A	0.0026	2.98E-07	7	Foerster 1968
	A	0.0021	3.26E-07	24	Peterman 1982
Karluk River	A	0.0017	7.86E-09	6	Barnaby 1944
Summit Lake	A	0.0036	1.73E-08	3	Roberson and Holder 1987
Ten Mile Lake	A	0.0032	2.88E-07	6	
Gulkana Hatchery	A	0.0031	7.65E-08	9	
Lake Washington	A	0.0034	4.42E-07	11	Thorne and Ames 1987
Oncorhynchus spp.	E	0.0147	2.90E-05	23	McNeil 1969
Pagrus pagrus	A	0.0012	7.76E-09	3	Manooch and Huntsman 1977
Perca flavescans	J	0.0146	2.36E-05	6	Forney 1971
	J	0.0320	1.53E-04	8	
	A	0.0079	8.90E-06	12	Nielson 1980
Plecoglossus altivelis	J	0.0097	6.70E-06	3	Kawanabe 1969
Pleuronectes platessa	E	0.0783	1.24E-03	11	Harding et al. 1978
	E	0.1165	4.70E-03	2	Heessen and Rijnsdorp 1989
	L	0.0525	7.24E-04	4	Bannister et al. 1974
	L	0.0112	6.46E-05	7	Zijlstra et al. 1982
	J	0.0336	7.69E-04	2	Al-Hossaini et al. 1989
Firemore	J	0.0303	1.07E-04	4	Lockwood 1980
Filey Bay	J	0.0245	1.18E-04	4	
	J	0.0030	1.08E-06	5	Zijlstra et al. 1982
Pseudopleuronectes americanus	J	0.0389	1.09E-04	3	Howe et al. 1976
	J	0.0058	3.04E-07	2	Pearcy 1962
	A	0.0019	1.18E-07	5	Poole 1969
Salmo salar	J	0.0019	7.07E-07	7	Chadwick 1982
	J	0.0027	1.38E-07	10	Chadwick 1987
	A	0.0058	2.36E-06	9	
Salvelinus alpinus	A	0.0015	1.53E-06	2	Jonsson et al. 1988
S. frontinalis	J	0.0082	6.47E-06	6	Shetter 1961
	J	0.0110	8.76E-07	9	
	J	0.0106	1.55E-07	3	
S. salvelinus	A	0.0042	4.59E-06	5	Alexander and Shetter 1969
Sardinops caerulea	L	0.0831	3.32E-04	2	Ahlstrom 1954
Scomber scomber	E	0.5260	2.50E-02	4	Ware and Lambert 1985
	L	0.5110	2.12E-02	3	
Sebastes spp.	L	0.0680	1.25E-03	2	Anderson 1984
Trachurus symmetrichus	L	0.1387	4.62E-04	3	Farris 1960

Post-yolksac larval development of two southern California sculpins, *Clinocottus analis* and *Orthonopias triacis* (Pisces: Cottidae)

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Abstract. – Complete series of field-collected larvae were used to describe the post-yolksac development of two common southern California marine sculpins, *Clinocottus analis* and *Orthonopias triacis*. Characters diagnostic of *C. analis* include nape pigment, dorsal head pigment, heavy rows of dorsal gut melanophores, 18–33 postanal ventral melanophores (PAVM). Postflexion larvae develop multiple preopercular spines (9–12) and several post-temporal/supracleithral spines, and later stages also acquire a W-shaped patch of pigment on the body under the second dorsal fin. Characters diagnostic of *Orthonopias triacis* include a heavy cap of dorsoposterior gut pigment, 26–55 PAVM, occasionally one or two dorsocranial melanophores, and, rarely, one melanophore at the nape; postflexion *O. triacis* develop four preopercular spines. Comparison with other cottid species is included.

Field collection data (1978–85) indicate *C. analis* and *O. triacis* larvae both occur in greatest densities off rocky habitats along the 15 m isobath. A key is provided for known preflexion marine sculpin larvae found in southern California.

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Clinocottus analis and *Orthonopias triacis* are two common marine sculpins (Pisces: Cottidae) of the rocky intertidal and subtidal areas of southern California (Miller and Lea 1972, Eschmeyer et al. 1983). The range of *C. analis* extends from Cape Mendocino, northern California, to Asuncion Pt., Baja California Sur; *O. triacis* extends from Monterey, central California, to San Geronimo I., central Baja California (Fig. 1).

A description of the embryology and larval development of *Clinocottus analis* was first attempted by Eigenmann (1892) who gave a preliminary description of the eggs and yolksac larvae of *C. analis* from reared eggs obtained in San Diego Bay CA, and subsequently by Budd (1940) from eggs obtained in Monterey Bay CA. In both studies the larvae died at the end of the yolksac stage. Bolin (1941) described the embryology and yolksac development of reared *Orthonopias triacis*.

Hubbs (1966) described many characteristics of *C. analis* embryology, especially in response to temperature, but gave no description of the larvae. Washington (1986) presented a description of a limited series of postflexion *C. analis* larvae and juveniles identified on the basis of meristic and morphological characters. A 7.0 mm *O. triacis* was previously illustrated (Washington et al. 1984). No description, however, of a complete larval series of either species exists, despite the common occurrence of adults in California coastal waters and the existence of several partial descriptions of their larval development in the literature.

The following is a description of larval series for both *C. analis* and *O. triacis* based on field-collected specimens from southern California and Baja California, Mexico. Comparison with other cottid species and occurrence is discussed. A key to known southern California preflexion cottid larvae is included to summarize early-life-history information from many sources including Richardson and Washington (1980), Richardson (1981), Washington et al. (1984), Washington (1986), Feeney (1987), and Matarese et al. (1989). This work is intended to aid in identification and hopefully stimulate further research on the development of related species.

Materials and methods

A total of 145 larvae and 9 juveniles of *Clinocottus analis* and 322 larvae and 4 juveniles of *Orthonopias triacis* were studied. Specimens were examined from the Scripps Vertebrate Collection (SIO), the Southwest Fisheries Science Center (SWFSC), the California Academy of Sciences (CAS), and the Natural History Museum of Los Angeles County, Section of Fishes (LACM).

The SIO specimens (21) are preserved in 50% isopropanol and were collected in Baja California at Bahia Todos Santos (SIO H51-19B); the lot

Figure 1
Geographic range of *Clinocottus analis* and *Orthonopias triacis*.

contained an excellent series of both *C. analis* and *O. triacis* postflexion larvae, the discovery of which became the impetus for the present study.

The SWFSC material (10 specimens) is preserved in 5% formalin; some specimens (6) were collected in Baja (6607-AX-110.32; 6806-JD-110.32; SWFSC/SIO H51-106), the remainder were collected in California. Two *C. analis* specimens (SWFSC/SIO H46-63) and two *O. triacis* (SWFSC 6607-AX-110.32) were cleared and stained.

CAS material included one lot of postflexion *C. analis* (SU 68789, 70% ethanol), collected in Monterey Bay, California.

LACM specimens (fixed in 5% formalin and preserved in either 5% formalin or 70% ethanol) were collected in coastal waters (<75 m depth) of the Southern California Bight between Pt. Conception and the Mexican border. Most specimens were collected during the Coastal Resources and 316b phases of the Ichthyoplankton Coastal and Harbor Studies (ICHS) Program and during the Bightwide Program; methods and station locations can be found in Brewer et al. (1981), Brewer and Smith (1982), and Lavenberg et al. (1986). Also, five postflexion *C. analis* specimens (LACM 45404-1, 45414-1–45417-1; in ethanol) were collected at the Catalina Island Marine Science Center (Ninos 1984). Six additional *C. analis* juveniles from the general LACM collection were used: four collected at Santa Barbara Island (LACM 31546-4), one at Catalina Island (LACM 35695-1), and one at Palos Verdes Peninsula (LACM 1993).

Morphometric data, including preanal length, body depth, pectoral length, head length, and eye diameter were measured from 50 *C. analis* and 54 *O. triacis* specimens. Data were entered into an "Excel" spreadsheet program on a Macintosh IIci. Means and standard deviation of morphometric measurements were computed using "SYSTAT." Frequency plots of melanophores vs. length were made using "SYGRAPH" and the "LOWESS" (locally-weighted least squares) scatterplot smoothing method (Wilkinson 1989).

Specimens were illustrated using a camera lucida attached to a Wild M3 stereomicroscope.

Occurrence data are based on specimens taken during 1978–85 on ICHS and Bightwide cruises using a variety of sampling gears. During Coastal Resources collections (ICHS cruises, 1978–79) oblique bongo samples and discrete depth samples were taken monthly along a grid of 10 transects, each with 4 stations. The transects were evenly spaced along the coast from Point Conception to San Diego. The stations corresponded to bottom depths of 8, 15, 22, and 36 m. Additionally, 8 stations (4 sites each) were located in Los Angeles–Long Beach Harbor and San Diego Bay. Integrated water-column samples were collected by fishing a 70 cm bongo sampler from the bottom to the surface. Discrete depth samples were collected at the surface (manta sampler), at the mid-depth of the water column (70 cm bongo sampler) and at the bottom (70 cm bongo sampler equipped with wheels). All samplers had nets of 335 μ mesh Nitex, and attached flowmeters gave estimates of the volume of water filtered. During the 316b phase (ICHS cruises, 1979–80) the number of transects was increased to 20 and the number of stations was reduced to 2 (8 and 22 m) except for 4 "expanded" transects (Ormond Beach, Playa del Rey, Seal Beach, San Onofre), which retained 4 stations (8, 15, 22, and 36 m). For epibenthic sampling, the benthic bongo sampler was replaced by a larger "Auriga" sampler. Collections were taken monthly during the 316b phase. Samples were sporadically taken in 1981, but no data from them are used here.

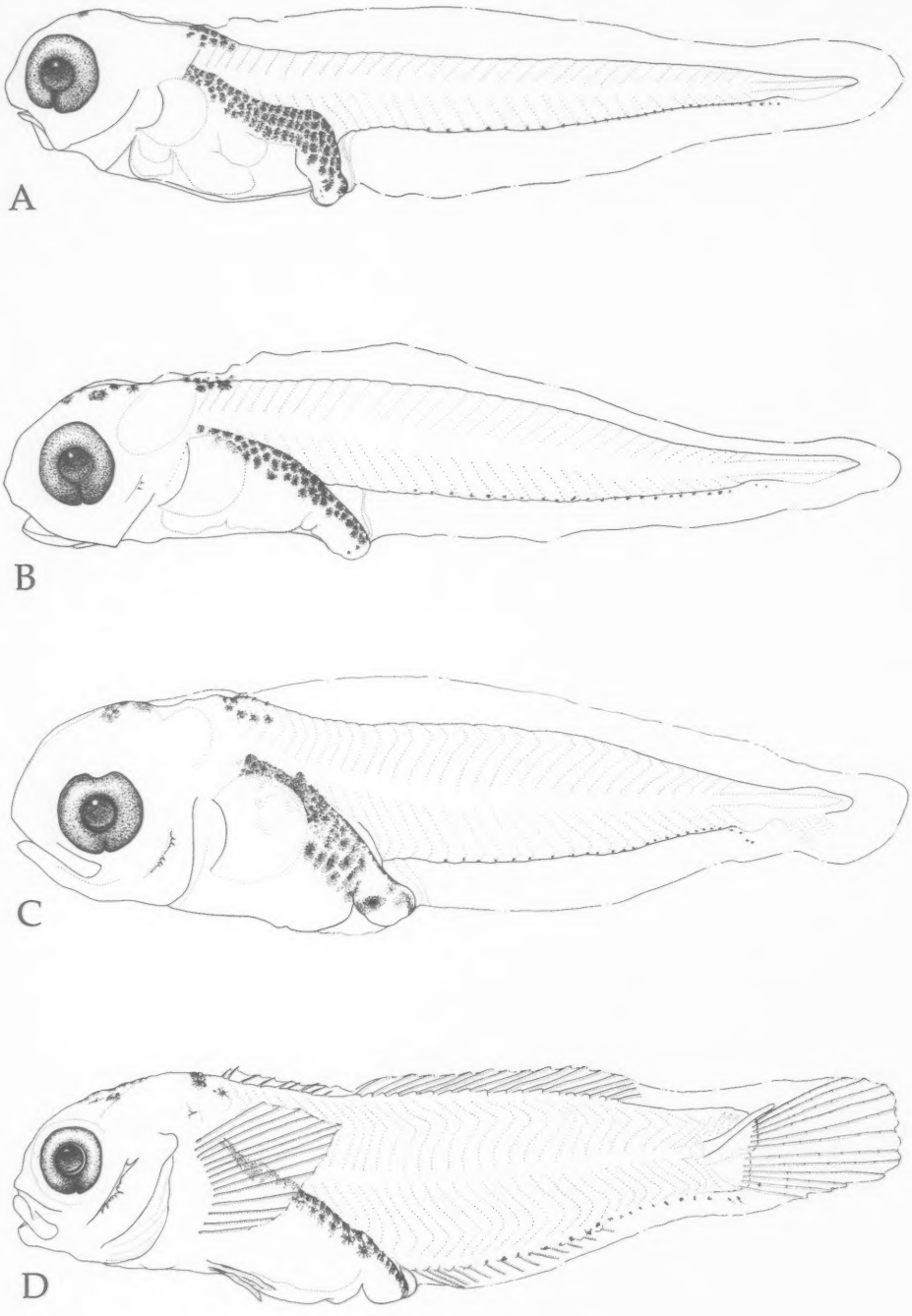

Figure 2

Field-collected *Clinocottus analis* larvae: (A) 3.9 mm (LACM KH #22), (B) 5.6 mm (LACM KH #22), (C) 5.6 mm (LACM 018-SO-36-AU-01), (D) 8.6 mm (SIO H51-19B).

The Bightwide program began in 1982 and samples were taken bimonthly at the four "expanded" 316b transects. During the Bightwide program, a fifth station (75 m) was added to each transect. Only oblique bongo samples were taken during the Bightwide phase. Additional details are provided in Lavenberg et al. (1986).

Estimates of larval abundance ($n/10\,m^2$ of sea surface) for each taxon were estimated (for methods, see Smith and Richardson 1977). These abundances were plotted against variables, such as transect, station depth, gear type and date, to determine patterns of local occurrence.

Identification

Yolksac and small post-yolksac larvae of *Clinocottus analis* and *Orthonopias triacis* were identified by comparison with descriptions of reared larvae (Eigenmann 1892, Budd 1940, Bolin 1941). Larger preflexion and flexion larvae were associated to postflexion larvae and juveniles using pigment characters, number of preopercular spines, length of gut, and location of the anus. Washington (1986) was helpful in linking postflexion *C. analis* individuals to juveniles using melanophore patterns and meristics. For definition of terms, see Feeney (1987).

Table 1
Morphometrics of larvae and juveniles of *Clinocottus analis* and *Orthonopias triacis*, represented as a mean percentage of standard length ± the standard deviation, with range in parentheses.

Measurement stage	*Clinocottus analis*	*Orthonopias triacis*
Preanal length		
Preflexion	46.0±3.4(40.0–52.2)	38.8±3.0(31.5–44.8)
Flexion	47.1±2.2(44.6–48.5)	41.7±2.8(37.8–47.2)
Postflexion	50.5±2.1(46.9–54.5)	43.5±3.0(39.1–48.3)
Juvenile	47.3±1.1(46.0–48.4)	43.5±2.7(39.9–46.3)
Body depth		
Preflexion	24.8±2.2(19.7–29.7)	24.3±3.1(19.8–33.2)
Flexion	23.8±2.2(21.3–25.3)	24.3±2.9(19.8–28.5)
Postflexion	28.7±2.0(25.6–32.7)	25.9±2.4(22.1–29.5)
Juvenile	26.4±2.7(24.5–30.4)	23.6±1.6(21.7–25.3)
Pectoral length		
Preflexion	8.5±1.3 (6.6–11.3)	8.1±1.2 (6.1–11.3)
Flexion	8.9±2.0 (7.3–11.2)	10.2±2.6 (6.3–16.0)
Postflexion	27.8±4.3(16.9–32.5)	18.2±5.0(10.8–25.4)
Juvenile	35.4±1.8(33.0–36.8)	34.9±2.0(32.4–37.1)
Head length		
Preflexion	21.8±2.1(18.6–26.1)	21.2±1.7(18.0–24.4)
Flexion	23.3±0.7(22.5–23.8)	24.1±2.7(19.3–29.1)
Postflexion	30.2±1.8(25.6–32.8)	28.0±2.3(25.0–31.4)
Juvenile	36.6±4.4(33.8–43.2)	34.5±1.3(33.1–35.7)
Eye diameter		
Preflexion	10.7±1.1 (8.3–12.5)	10.0±0.8 (8.5–12.2)
Flexion	10.1±0.2 (9.9–10.2)	9.2±0.9 (7.8–10.7)
Postflexion	8.9±0.6 (8.0–10.5)	9.1±1.1 (8.1–10.8)
Juvenile	10.0±0.6 (9.4–10.7)	10.9±1.1 (9.9–12.4)

Results

Description of *Clinocottus analis* larvae

Distinguishing characters Distinguishing characters of *Clinocottus analis* preflexion larvae include heavy dorsoposterior gut pigment, nape pigment (usually with a nape bubble), 18–25 postanal ventral melanophores (PAVM), and melanophores on the head over the midbrain. Late preflexion larvae may develop up to 33 PAVM. Larger flexion and postflexion larvae develop multiple preopercular spines (9–12) similar to other *Clinocottus* and *Oligocottus* species (Washington 1986). Transforming larvae develop a W-shaped patch of pigment under the 2d dorsal and have an advanced anus. In juveniles, the preopercular spines coalesce to one bifurcate spine; small, prickly scales begin to develop under the 2d dorsal fin. The anus advances about halfway to pelvic fin origin.

Morphology *Clinocottus analis* yolksac larvae hatch at lengths of 3.7–4.5 mm (Eigenmann 1892, Budd 1940); preserved field-collected larvae are found as small as 3.1 mm (due to shrinkage during preservation). Larvae are robust with fully pigmented eyes at hatching. Dorsal gut diverticulae (wings) as seen in some *Artedius* (Washington 1986) are absent; however, sometimes a bump can be seen in that area.

The preanal length averages 46% of notochordal length (NL), which is closer to Eigenmann's illustration (est. 44%) than to Budd's illustration (est. 33%); the minimum preanal length from field-collected specimens was 40% NL (Table 1). During flexion the preanal length increases slightly to an average of 47%. In postflexion larvae, preanal length increases to an average 51.5% standard length (SL). In juveniles, the pectoral fin and head lengthen to an average 35 and 37% SL, respectively (Table 1).

In postflexion larvae, the anus is slightly advanced of the anal fin origin. In transforming postflexion larvae, the anus advances from the anal fin to about one-third the distance to the pelvic fin origin. In juveniles, the anus advances almost halfway to the pelvic fins.

At 9.8 mm a cirrus appears on each dorsal orbit (Fig. 3B).

Fin development In postflexion larvae, fin elements start to form; the caudal rays become segmented. Pelvic fins appear as buds (Table 2). At 9.8 mm, fin rays, including the pelvics, are well-formed.

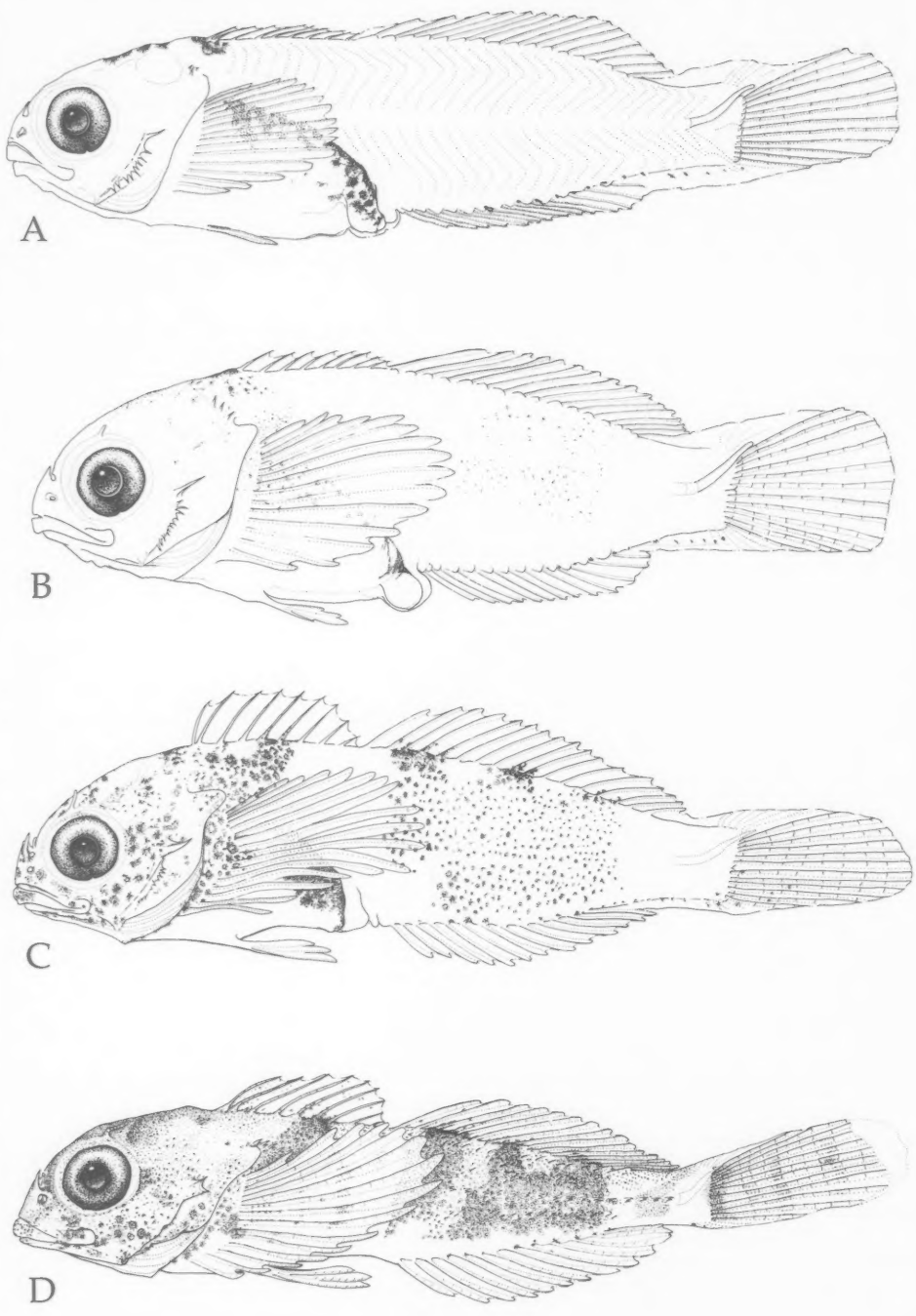

Figure 3

Field-collected *Clinocottus analis* larvae and juveniles: (A) 9.7 mm (SIO H51-19B), (B) 9.8 mm (SIO H51-19B), (C) 10.6 mm (LACM 008-88-22-MA-01), (D) 13.3 mm (LACM 45404-1).

Spination Preopercular spines begin to develop in the late preflexion stage at ~5.5 mm NL; the 5.6 mm specimen (in Fig. 2B) has developed 2 spines. During flexion, the number of preopercular spines increases to 5 (Table 2, Fig. 2C).

In postflexion larvae, the preopercular spines number 6–12 (Table 2); the upper spine is elongated. A post-temporal/supracleithral spine appears at 8 mm (Fig. 2D).

By 9.7 mm, a pair of nasal spines appear (Fig. 3A). The dorsalmost preopercular spine elongates to about twice the length of other spines. The number of post-temporal/supracleithral spines increases to 3. At 9.8 mm, a small spine (not illustrated) may be present where the sensory canal forms over the parietal, anterior to the nape; the spine persists in specimens up to 11 mm SL (CAS SU 68789).

In juveniles, multiple preopercle spines (about 10) coalesce to 1 elongate, bifurcated uppermost spine and 2 convex undulations ventrally where the other spines had been. Larval post-temporal spines form the anteriormost part of the lateral line which later becomes decorated with a series of multispined scales. Smaller spines (prickles) form laterally below the 2d dorsal and lateral line.

Pigmentation In yolksac *Clinocottus analis*, about 140 dense melanophores in 6–7 rows line the dorsoposterior gut (peritoneal) membrane (Eigenmann 1892, Budd 1940). Nape melanophores number 11–15 with several extending onto a bubble of skin that is usually present at the anterior nape. A stellate melanophore can usually be found on the head over one or both sides of the midbrain. A row of 18–25 PAVM is present from about the 6th postanal myomere to the caudal area; the last 2–3 melanophores usually extend down into the finfold.

Post-yolksac larvae retain much of the appearance of the yolksac larvae (Fig. 2A). The number of PAVM may increase to 33, but usually ranges in the mid-20s, generally decreasing in larger larvae (Fig. 4).

Late preflexion larvae develop numerous head melanophores over the midbrain (Fig. 2B). One 4.6 mm specimen had 19 midbrain melanophores and one forebrain melanophore; however, the melanophores over the midbrain usually number 10–15 with no forebrain pigment. Melanophores sometimes form at the anus in this stage; however, these usually form in the postflexion stage. One 5.2 mm specimen had 5–6 melanophores in a circle around the anus.

By 9.7 mm, the number of PAVM has decreased to less than 23 (Fig. 4). In a 9.8 mm specimen (Fig. 3B), melanophores begin to form below the nape and laterally below the second dorsal fin.

Table 2

Meristics of larvae and juveniles of *Clinocottus analis* (specimens inside the two dashed lines are undergoing flexion of the notochord).

Size (mm)	D_1	D_2	A	P	V	PS	PCV	CV	TV	M	PAVM
3.1	—	—	—	—	—	0	—	—	—	35	29
4.2	—	—	—	—	—	0	—	—	—	33	28
5.6	—	—	—	—	—	2	—	—	—	34	24
5.2	—	—	—	—	—	?	—	—	—	34	25
5.6	—	—	—	—	—	5?	—	—	—	34	26
8.4	IX?	17?	13	15?	buds	6–8	—	—	—	32	21
9.7	IX	16	14	15	I,3	10	—	—	—	33	14
10.5	IX	17	14	15	I,3	10	—	—	—	31?	17?
10.9*	IX	17	13	15	I,3	11?	11	22	33	—	—
11.1	IX	17	13	15	I,3	9	—	—	—	32	9
11.4*	IX	17	14	15	I,3	11	11	22	33	—	—
13.3**	IX	16	13	15	I,3	1	11	21	32	—	11
15.1	IX	16	13	15	I,3	1†	—	—	—	—	14
15.8**	IX	16	13	15	I,3	1	11	21	32	—	8
21.0	IX	16	13	15	I,3	1†	—	—	—	—	8

D_1 dorsal fin spines
D_2 dorsal rays
A anal fin rays
P pectoral fin rays
V pelvic rays
PS preopercle spines
PCV precaudal vertebrae
CV caudal vertebrae
TV total vertebrae
M myomeres
PAVM postanal ventral melanophores

*cleared and stained larvae
**x-rayed
†The one preopercle spine has a double point.

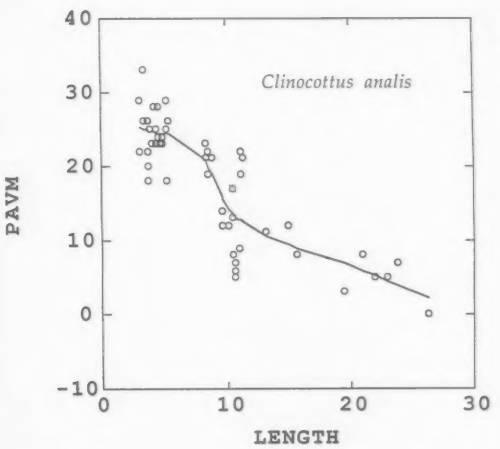

Figure 4

Frequency of postanal ventral melanophores (PAVM) vs. length (mm) with a LOWESS regression line at F = 0.5 (half the points included in a running window) for *Clinocottus analis* larvae and juveniles.

Transforming postflexion larvae develop a wide band of pigment under the second dorsal that is typically W-shaped and extends ventrally almost to the anal fin (Fig. 3C). Another band of dense pigment forms under the first dorsal fin and extends down across and onto the pectoral fin base. The head becomes heavily pigmented; about 15 large stellate melanophores (along with numerous small ones) extend across the preopercle and below the eye. Two or three melanophores appear on the posterior maxillary. Melanophores surround the nasal openings and spine. A band of pigment runs across the anterior upper lip (premaxillary). The lower jaw and chin also have pigment. The ventral gut is not pigmented. Several of the caudal rays are pigmented.

Juvenile *C. analis* continue to add pigment dorsolaterally while still retaining some of the larval pigmentation (Fig. 3D). The W-shaped patch is still present under the second dorsal, as well as a band of pigment under the first dorsal and across the pectoral fin base. The number of PAVM continue to decrease (Fig. 4). Two new patches of melanophores appear on the caudal peduncle and over the hypural plates. Melanophores appear in the dorsal, pectoral and caudal fins.

Meristics *Clinocottus analis* postflexion larvae have 6 branchiostegal rays and twelve (6+6) principal caudal rays which are consistent with adult counts. Other meristics are given in Table 2. Numbers of fin and vertebral elements match well with modes given by Howe and Richardson (1978).

Comparison with other species

Clinocottus analis larvae have no anterior gut pigment like *C. recalvus* larvae (Morris, 1951). *Clinocottus acuticeps* also has forebrain pigment and a longer trailing gut than *C. analis*, no early head pigment, fewer PAVM, and hindgut diverticulae (Washington 1986). *Clinocottus embryum* has fewer nape and PAVM. *Clinocottus globiceps* has anterior gut pigment and only four or five PAVM.

Preflexion *Oligocottus maculosus* have shorter guts (preanal averages 39.1% SL) than *C. analis* (Washington 1986). *Oligocottus snyderi* has no head pigment and few PAVM (~6). Larvae of *O. rubellio* (rosy sculpin) and *O. rimensis* (saddleback sculpin) have not been described. A 15.6mm juvenile *O. rubellio* (LACM 42918-1) differs from *C. analis* juveniles by having more cirri on the head, no W-shaped pigment patch laterally, and no banding anywhere, just a fine covering of light melanophores. *Oligocottus rimensis* differs by having an elongate body and a high number of dorsal soft rays (16–19). A 17.1mm *O. rimensis* (LACM 943) is developing saddles of pigment typical of adults but lacks the W-shaped patch of *C. analis*. *Oligocottus rimensis* has a single large preopercular spine (single pointed) and 3 smaller spines, similar to the "*Myoxocephalus*" group (Washington et al. 1984), i.e., 4 preopercle spines throughout their early development; the dorsal spine elongates in juveniles. *Oliocottus rimensis* juveniles also have no head cirri and the first pelvic ray appears double (split in two).

Clinocottus analis differs from some *Artedius* (*A. fenestralis*, *A. lateralis*, *A.* spp.) by having no large gut diverticulae (wings). Species of *Artedius* without wings (*A. creaseri*) differ by having anterior gut pigment and fewer PAVM (~10) (See Appendix 1).

Occurrence

Oblique bongo samples from coastal waters (8, 15, 22, 36, and 75m depths) of the Southern California Bight taken during the period 1978–84 (see Lavenberg et al. (1986) for methods) indicate *C. analis* larvae (mostly preflexion) were captured at the greatest densities along the 15m isobath off rocky tidepool areas in southern California, especially off Palos Verdes Peninsula and Gaviota in 1979–80. Larvae occurred during all months of the year, with peak abundance in July. Wells (1986) found that *C. analis* spawn throughout the year, with a peak in September–November in 1971–72, based on gonosomatic index values and the appearance of juveniles in the tidepools.

In discrete depth (neuston, middepth, epibenthic) samples taken in the Southern California Bight in October 1978 and June 1979–July 1980, 100% of the *C. analis* larvae (almost exclusively notochordal and flexion sizes) were caught in epibenthic samplers (benthic bongo or auriga nets) indicating the smaller larvae are near the bottom. Large postflexion individuals were common in neuston tows (manta nets) taken during the Coastal Resources Program (1978–79 except October; not fully sorted to date) at Coho Bay (Pt. Conception), and Playa del Rey and Seal Beach (stations on each side of Palos Verdes; no station at Palos Verdes) indicating larger postflexion, metamorphosing larvae are located near the surface. Ninos (1984) collected many larger postflexion larvae (~10mm) during surface night-lighting at Catalina Island. At Palos Verdes, juveniles (<25mm) are found back in the intertidal in small pools, separated from the larger adults (Wells 1986).

Description of *Orthonopias triacis* larvae

Distinguishing characters Distinguishing characters for *Orthonopias triacis* larvae include a heavy cap of pigment on the dorsoposterior gut, 26–55 PAVM, nape melanophores usually absent, no wings, short gut

(preanal length 31.5–44.8% SL in preflexion larvae), and 4 preopercular spines in late-flexion and postflexion larvae. Postflexion larvae and juveniles have an anus advanced from the anal fin. Juveniles develop rows of spiny scales between the dorsal fin and lateral line.

Morphology *Orthonopias triacis* larvae hatch at 2.9–3.8mm (Bolin 1941); field-collected larvae are as small as 2.6mm (after preservation). At 4.3mm, the caudal fin anlage is forming (Fig. 5B). Flexion occurs in larvae between 4.2 and 7.2mm (Table 3).

In preflexion larvae, the preanal length averages 39% SL (Table 1). During flexion the preanal length increases to an average of 42% SL. Postflexion preanal length averages 43.5% SL. Small juveniles (13.2mm, LACM W67-153, not illustrated) also have an average preanal distance of 43.5% SL.

In postflexion larvae, the anus starts to advance anteriorly from the developing anal fin. In larger postflexion larvae (Fig. 6C), a cirrus forms on the orbit. Small juveniles (13.2mm, LACM W67-153, not illustrated) have a cirrus on the orbit and one in the interorbital space; they also have lateral line scales and scale bands under the dorsal fin.

Larger juveniles (Fig. 6D) have numerous cirri and spines on the head; a smaller cirrus forms on the maxillary and cirri develop between the preopercular spines. The anus is located about halfway to pelvic origin.

Fin development In postflexion larvae, complete rays are formed by 7.2mm in all fins except the pelvics, which are present as buds (Table 3).

Spination Preopercular spines start to form in *Orthonopias triacis* during flexion at 4.2–5.8mm (Fig. 5C, Table 3). Postflexion larvae typically have 4 preopercular spines of about equal size and equally spaced (Fig. 6B). Sometimes an accessory preopercular spine is present; a 7.3mm larva possesses a smaller spine adjacent to the 2 large spine from the top.

Small juveniles (13.2mm, LACM W67-153, not illustrated) still retain the 4 preopercular spines (Table 3). In larger juveniles (Fig. 6D, Table 3), preopercular spines are reduced to 3 and a bump where the ventralmost one used to be; the dorsalmost spine becomes bifurcate.

In large postflexion larvae (Fig. 6C), nasal spines are present. Three post-temporal/supracleithral spines appear above the opercular flap near the point where the lateral line will start to form. A small foramen is present on the parietals where a sensory canal forms.

Table 3

Meristics of larvae and juveniles of *Orthonopias triacis* (specimens inside the two dashed lines are undergoing flexion of the notochord).

Size (mm)	D_1	D_2	A	P	V	PS	PCV	CV	TV	M	PAVM
2.6	—	—	—	—	—	0	—	—	—	34	40
3.4	—	—	—	—	—	0	—	—	—	36	51
4.3	—	—	—	—	—	0	—	—	—	36	30
4.2	—	—	—	—	—	1	—	—	—	37?	43
4.9	—	—	—	—	—	2	—	—	—	34	35
5.5	—	—	—	—	—	2	—	—	—	35	35
6.5	—	—	—	—	—	4	—	—	—	35	27
7.2	—	—	—	—	—	4	—	—	—	34	28
6.8	IX?	16?	11?	14?	buds	5*	—	—	—	34	25
7.3	IX?	16?	12?	14?	buds	4	—	—	—	35	33
8.2**	IX	16	12	14	I,3	4	11	24	35	—	—
9.2	IX	16	12	14	I,3	4	—	—	—	35	7?
13.2	IX	17	12	15	I,3	4	—	—	—	—	1
17.2	IX	17	12	14	I,3	4	—	—	—	—	0
23.0†	IX	17	12	14	I,3	3††	11	24	35	—	8

* Second (from dorsum) preopercle spine has smaller spine next to it.
** cleared and stained larvae
† x-rayed
†† Dorsal preopercle spine has a double point.

Pigmentation Yolksac *Orthonopias triacis* have pigmented eyes at hatching, a cap of dense pigment on the dorsoposterior gut, and about 35 PAVM that start on the 3d or 4th postanal myomere. One or a pair of head melanophores is sometimes present (Bolin 1941).

The dorsoposterior gut pigment in field-collected larvae is composed of ~80–90 melanophores in a circular pattern (Fig. 5A). Small larvae (<4mm) have 32–55 PAVM (Fig. 7); preflexion larvae >4mm have 26–43 PAVM. One or two head melanophores over the midbrain occur in about 33% of preflexion larvae. Nape pigment is usually absent; one punctate melanophore occurs at the nape in about 25% of preflexion larvae.

Flexion larvae have similar pigment as above (Fig. 5D, 6A). The first few PAVM are formed as dashes of pigment at the start of the anal fin base (Fig. 6A). A 7.0mm specimen (Washington et al. 1984) has at least 3 head melanophores and 1 nape melanophore, and seems to be just completing flexion. A 5.8mm specimen (that may have shrunk to a greater extent because it was ETOH-preserved) completing flexion has 12 head melanophores and 2 nape melanophores (LACM 009-80-36-BB-01).

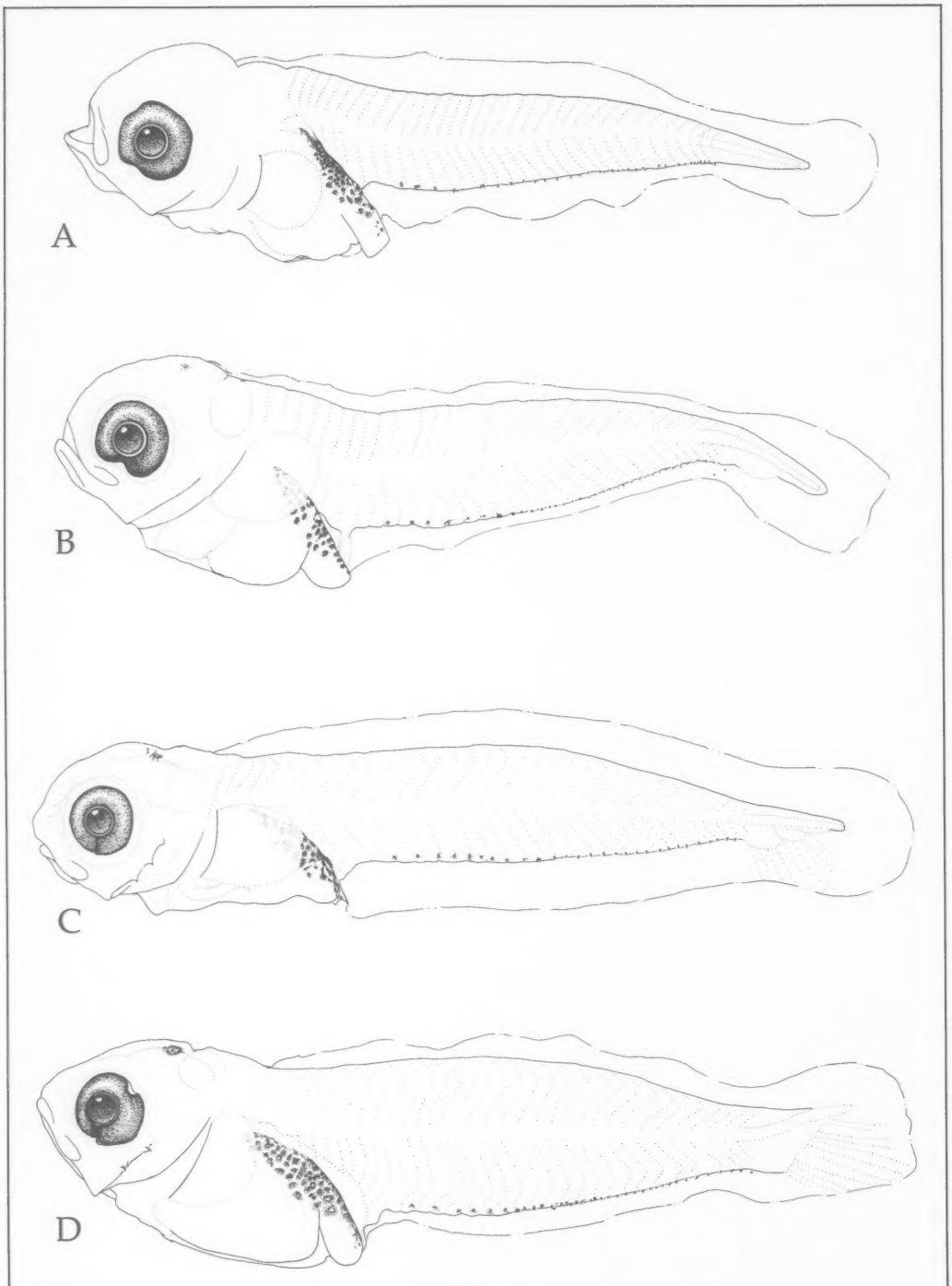

Figure 5

Field-collected *Orthonopias triacis* larvae: (A) 3.3 mm (LACM 026-PV-22-OB-02p), (B) 4.3 mm (LACM 026-PV-15-OB-01p), (C) 5.8 mm (SIO H51-19B), (D) 5.5 mm (LACM 012-80-08-BB-01).

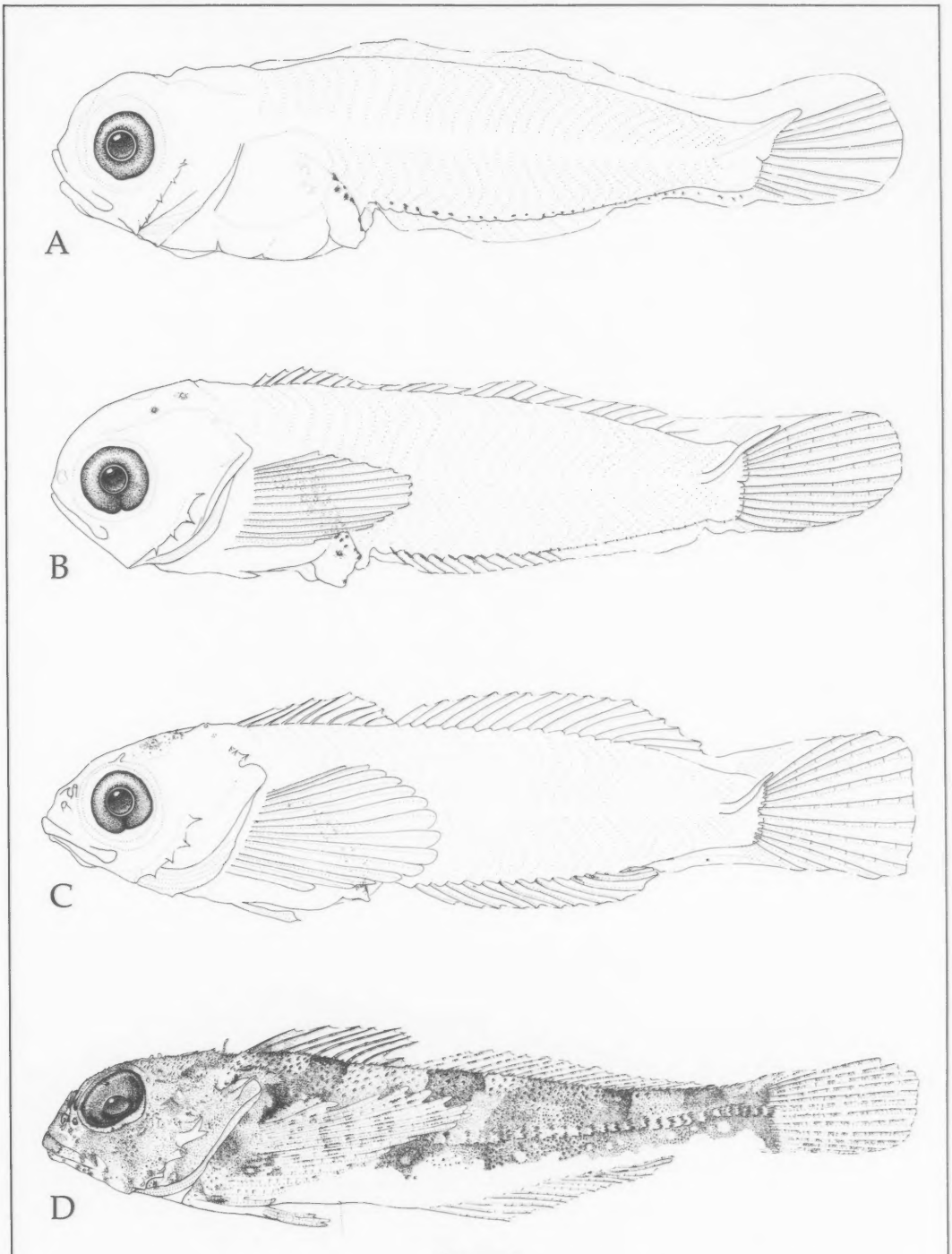

Figure 6

Field-collected *Orthonopias triacis* larvae and juveniles: (A) 5.9mm (LACM 026-PV-15-OB-01p), (B) 7.2mm (LACM 012-88-36-BB-01), (C) 9.2mm (SIO H51-19B), (D) 23.0mm (LACM 9423-8).

Postflexion PAVM pigment takes the form of dashes at the base of each anal ray. At least 3 melanophores can be found on the head over the midbrain. In larger postflexion larvae, the number of PAVM is greatly reduced (Fig. 7).

Small juveniles (13.2mm, LACM W67-153, not illustrated) have numerous melanophores over the midbrain. Few or no PAVM may be present (Fig. 7). In the 13.2mm juvenile, a dark patch of melanophores on the pectoral fin base extends to and around the pelvic girdle and meets at the ventral midline. Bands of pigment extend down from the dorsum and stop just ventral to lateral line.

In larger juveniles (Fig. 6D) a patch of melanophores is present on the pectoral fin base, but may not be continuous across the pelvic girdle as it is in the 13.2mm juvenile. Light circles appear in the dense pigment below the lateral line.

Meristics Meristics for *O. triacis* (Table 3) are comparable to published accounts. Modes for the fin elements matched those given in Howe and Richardson (1978). Vertebrae (35) were 1 greater than the mode (34) in Howe and Richardson. Branchiostegal rays (BR) form during flexion; a 5.6mmFL larva had 5 visible BR. In postlarvae and juveniles, branchiostegal rays = 6, PCR = 6+6.

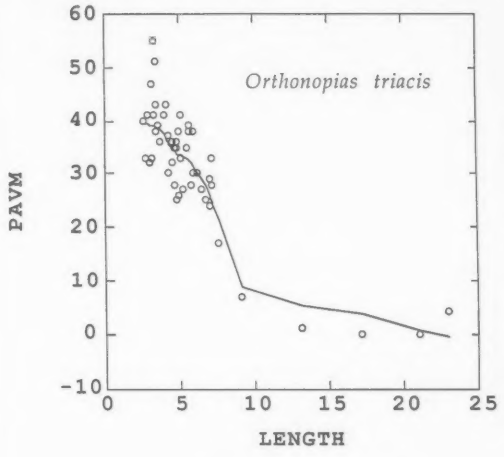

Figure 7
Frequency of postanal ventral melanophores (PAVM) vs. length (mm) with a LOWESS regression line at F = 0.5 (half the points included in a running window) for *Orthonopias triacis* larvae and juveniles.

Comparison with other species

Orthonopias triacis are similar to *Artedius meanyi* larvae (Washington 1986) by possession of 4 preopercular spines, a short compact gut, and an eye cirrus; *A. meanyi* postflexion larvae and juveniles also develop small, prickly scales on the head and below the dorsal fin. *Artedius meanyi* differ in having far fewer PAVM (<13), pigment in the dorsal finfold, anterior gut melanophores, and in undergoing flexion at a larger size (6.2–9.4mm). *Artedius meanyi* and *O. triacis* were put in the "*Myoxocephalus*" group by Washington et al. (1984) due to the presence of 4 preopercular spines.

Orthonopias triacis larvae are similar to others within the "*Myoxocephalus*" group, including *Icelinus* and *Chitonotus*, in having no heavy nape pigment and a high number of PAVM; *Icelinus quadriseriatus* has 25–63 PAVM (Feeney 1987) and *Chitonotus* has 24–45 PAVM (Richardson and Washington 1980). *Orthonopias triacis* lacks ventral gut pigment (see Appendix 1).

Orthonopias triacis can not be assigned to the "*Artedius/Clinocottus/Oligocottus*" group, as tentatively suggested by Richardson (1981), because it lacks the multiple preopercular spine pattern, gut diverticulae, and trailing gut. *Clinocottus analis* postflexion larvae (this paper) are similar to *O. triacis* because of the advanced anus and presence of head pigment, nasal spines, post-temporal/supracleithral spines, cirri over the eye, and similar meristics. *Clinocottus analis* differs in having multiple (>5) preopercular spines, a 'W' shaped pigment patch on the side of the body, and a longer gut (preanal = 46.0–54.5% SL vs. 39.1–48.3% SL in *O. triacis*).

Orthonopias triacis larvae initially have more PAVM than *C. analis*; however, the number of PAVM decreases with length more quickly than *C. analis* (Figs. 6, 7); linear regressions (not shown) of *O. triacis* PAVM have a greater negative slope (−2.413 vs. −1.161) than *C. analis*. Linear regression lines were not used, however, in the final plots (Figs. 6, 7) because LOWESS smoothing (Wilkinson 1989) indicates that the relationship between PAVM and length may be nonlinear, especially in *O. triacis*. Additional large postflexion and juvenile specimens need to be examined to verify this relationship.

Occurrence

During 1978–84, *O. triacis* larvae (like *C. analis*) were collected in highest densities off Palos Verdes and other rocky areas, at the 15m isobath during the entire year, peaking in spring and summer. Approximately 72% of the larvae in discrete depth tows were collected in epibenthic tows and none in neuston tows. Flexion larvae were rarely collected. Postflexion individuals have not been found in the 1978–79 neuston tows as were

C. analis. Postflexion/metamorphosing individuals apparently do not exhibit neustonic behavior like *C. analis*. Juvenile *O. triacis* have been collected subtidally on reefs and off rocky areas (LACM collection data).

Conclusions

Clinocottus analis larvae can be grouped with the "*Artedius*" group of cottid larvae based on the high number of preopercular spines (9–12) (Washington et al. 1984). The advanced anus of postflexion larvae is typical of *Clinocottus*. Swank (1988) showed that *Clinocottus analis* is more closely related to other species within the genus rather than to *Oligocottus maculosus*; *C. analis* was found to be the most divergent in the genus. Larval characters presented here lend support to her conclusions. *Clinocottus analis* larvae share many characters with other *Clinocottus*, but still have some significant differences, i.e., a high PAVM count and development of prickly spines on the body.

Orthonopias triacis larvae can be grouped, along with *A. creaseri*, *A. meanyi*, *Chitonotus*, and *Icelinus*, in the "*Myoxocephalus*" group (Washington et al. 1984) because of the presence of four preopercular spines. Body morphology of *O. triacis* is most similar to *A. meanyi*.

Orthonopias triacis and *C. analis* preflexion larvae co-occur in the same areas (15 m isobath near rocky habitats), but can be easily distinguished using pigment and morphological characters. Larger postflexion larvae can be distinguished by the number of preopercular spines.

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Appendix 1: Key to known southern California sculpin larvae (preflexion stage)

Comments: The following key is provided as a guide to identifying known Southern California sculpin larvae. Some larvae may not key out exactly due to variation in pigment or because they are a species that is not described yet (see table at end of key). Types (e.g., *Artedius* type 16) are named as they are labeled in the LACM collection. Equivalent types in literature are noted.

1	Wings (gut diverticulae) present	**2**
	Wings absent (or as bumps only)	**4**
2(1)	Postanal ventral melanophores 3–12	**3**
	Postanal ventral melanophores 22–32	***Artedius lateralis***
3(2)	Nape pigment present; myomeres 32–35 (= *Artedius* type 3 (Washington 1986); may be either *A. corallinus* or *A. notospilosus*)	***Artedius* type 16**
	Nape pigment absent; myomeres 36–37 (= undescribed; has wings like other *Artedius*, no nape pigment, and only 3–8 PAVM)	***Artedius* type A**
4(1)	Body covered with melanophores	**5**
	Body melanophores restricted to ventral midline, gut, nape or head region	**9**
5(4)	~26–28 myomeres; stubby body (hatches at 6–7 mm)	***Rhamphocottus richardsonii****
	36–41 myomeres; elongate body	**6**
6(5)	Elongate pectoral fin (>20% of the body); pigment extending into dorsal and anal finfold (hatches at ~7–9 mm)	***Nautichthys oculofasciatus****
	Pectoral fins not elongate (<15% of body); no pigment extending into fins	**7**
7(6)	Lateral body relatively unpigmented; preanal length 36–42% of notochordal length	***Hemilepidotus spinosus***
	Lateral body covered with melanophores; preanal length ~44–46% of notochordal length	**8**
8(7)	Series of elongate melanophores present along the lateral midline; pointed snout	***Radulinus* sp.**
	No distinct series of elongate melanophores along the lateral midline; blunt snout	***Scorpaenichthys marmoratus***
9(4)	Otic capsule pigment present (may be present in *Paricelinus hopliticus*)	**10**
	Otic capsule pigment absent	**11**

10(9) Nape pigment present (several melanophores); dorsal gut pigment not in bands ..... ***Oligocottus/Clinocottus* type D**
(= *C. recalvus* (Morris 1951) or *C. globiceps* or *O. maculosus* (Washington 1986). These specimens are most similar to larger *C. recalvus* from same locality; however, they share characters with all three species (e.g., otic capsule pigment) or with one species (e.g., nape bubble like *O. maculosus*).

Nape pigment absent (or 1 melanophore occipitally); dorsal gut pigment in bands ..... ***Leptocottus armatus***

11(9) Nape pigment present 12

Nape pigment absent (rarely present in *Orthonopias* triacis and flexon *Chitonotus pugetensis*) ... 19

12(11) Anterior gut pigment present; ventral gut pigment present 13

Anterior gut pigment absent; ventral gut pigment absent 14

13(12) Myomeres 40–42; postanal ventral melanophores ~37–38; pigment on snout ..... ***Paricelinus hopliticus****

Myomeres 27–30; postanal ventral melanophores <15; pigment on snout absent ..... ***Enophrys taurina?***
(= undescribed; only one specimen collected, similar to *E. bison* description (Richardson and Washington 1980) except for scattered ventral gut pigment)

14(12) Postanal ventral melanophores 5–14 15

Postanal ventral melanophores 15–33 16

15(14) Preanal myomeres 7–9; head pigment usually absent; gut pigment light and scattered ..... ***Oligocottus synderi***

Preanal myomeres 10–12; head pigment present; gut pigment heavy ..... ***Oligocottus/Clinocottus* type B**
(= undescribed; looks much like *C. analis* but has only 10–14 PAVM)

16(14) Nape melanophores <6 17

Nape melanophores >6 18

17(16) Postanal ventral melanophores 15–21; dorsal gut pigment light to moderate ..... ***Clinocottus embryum****

Postanal ventral melanophores 21–33; dorsal gut pigment heavy ..... ***Artedius harringtoni***

18(16) Head pigment absent; dorsal gut pigment moderate; nape melanophores ~18 ..... ***Oligocottus/Clinocottus* type C**
(= undescribed; no head pigment, 17–31 PAVM; lighter pigment than *C. analis*, may be *O. maculosus*)

Head pigment present (except in smallest larvae (<3.0 mm)); dorsal gut pigment heavy; nape melanophores <17 ..... ***Clinocottus analis***

19(11) Postanal ventral melanophores 7–18 20

Postanal ventral melanophores ≥24 21

20(19) Ventral gut pigment absent; preanal myomeres 8–10 ..... ***Artedius creaseri***

Ventral gut pigment present; preanal myomeres 11–12 ..... ***Cottus asper***

21(19) Ventral gut pigment present **22**

Ventral gut pigment absent ..... ***Orthonopias triacis***

22(21) ~5 parallel lines (striations) of pigment oriented horizontally on posterior gut .... ***Synchirus gilli****

No parallel lines of pigment on posterior gut **23**

23(22) Two or more prominent anterior gut melanophores present **24**

Anterior gut melanophores absent (or one only) **26**

24(23) Dorsal head pigment absent; jaw angle pigment present **25**

Dorsal head pigment present (except in larvae ~3.5 mm or smaller); jaw angle pigment usually absent ..... ***Chitonotus pugetensis***

25(24) Anterior gut melanophores ~2; myomeres 33–37 ..... ***Icelinus/Chitonotus***
(= not a type, but a category for ambiguous or damaged specimens that may be either *Icelinus* or *Chitonotus*)

Anterior gut melanophores ~10; myomeres 38–40 ..... ***Icelinus* type A**
(= undescribed; probably *I. tenuis* based on high myomere counts (38–40))

26(23) Jaw angle (quadrate) pigment present ..... ***Icelinus quadriseriatus***

Jaw angle pigment absent ..... ***Icelinus/Chitonotus***

*I have not examined larvae of this type; characters were taken from the literature.

Appendix table

The following larvae have not been described and are probably unknown, which should be taken into consideration when using the key, especially if the larva(e) do not key out exactly.

Taxa	Comments
Artedius corallinus	15–16 dorsal rays; *A.* type 3?; intertidal (see Washington 1986).
Artedius notospilotus	*A.* type 3? (Washington 1986).
Icelinus burchami fuscescens	Rare; found in deep water (126–549 m); 16–18 dorsal rays.
Icelinus cavifrons	X–XI dorsal spines (>98%); IX dorsal spines (<2%).
Icelinus filamentosus	15–18 dorsal rays.
Icelinus fimbriatus	Rare; found at moderate depths (60–265 m); X–XI dorsal spines.
Icelinus oculatus	Rare; found in deep water (109–274 m); X–XI dorsal spines; 37 vertebrae.
Icelinus sp. nov.	X dorsal spines; rare?
Leiocottus hirundo	16–17 dorsal rays; recent occurrence on reefs in Santa Barbara area and Santa Cruz I., California.
Oligocottus rimensis	16–19 dorsal rays; juveniles lack 'W'-shaped pigment on side; intertidal.
Oligocottus rubellio	Juveniles lack 'W'-shaped pigment on side; intertidal.
Psychrolutes phrictus	Rare, found in deep water (839–2800 m), 22–26 pectoral rays; may = "cottoid A" (Richardson and Washington 1980).
Radulinus vinculus	Rare; southern range limit is Anacapa I.
Zesticelus profundorum	Rare; 25–26 vertebrae; deep water (88–2580 m).

Abstract. – To investigate the genetic basis of stock structure of the weakfish *Cynoscion regalis*, a total of 370 individuals was collected from four geographic sites along the mid-Atlantic coast of the United States over a period of 4 years. Restriction fragment length polymorphism (RFLP) analysis of weakfish mitochondrial DNA, employing either 6 or 13 restriction endonucleases, demonstrated a low level of intraspecific mtDNA variation, with a mean nucleotide sequence divergence of 0.13% for the pooled samples. The common mtDNA genotype occurred at a frequency of 0.91–0.96 in all samples, and no significant heterogeneity was found among samples in the occurrence of the common mtDNA genotype or rare variants. The lack of spatial partitioning of rare mtDNA genotypes among collection sites suggests considerable gene flow along the mid-Atlantic coast. Together these data are consistent with the hypothesis that weakfish comprise a single gene pool, and indicate that the fishery should be managed as a single, interdependent unit.

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A genetic analysis of weakfish *Cynoscion regalis* stock structure along the mid-Atlantic Coast*

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The weakfish *Cynoscion regalis* is broadly distributed along the Atlantic coast of the United States. It is common from Long Island NY to Cape Canaveral FL, and has occasionally been reported from as far north as Nova Scotia and as far south as the Gulf of Mexico (Bigelow and Schroeder 1953, Weinstein and Yerger 1976). Weakfish abundance varies considerably on both a spatial and temporal basis, especially in the northern part of the species' range (Bigelow and Schroeder 1953).

The life history of the weakfish has been well studied (reviewed in Wilk 1979). Spawning occurs in estuarine and coastal waters from late spring through early fall, with a peak of activity in late May and early June. There appears to be little offshore transport of the early-life-history stages, and young-of-the-year remain in shallow estuarine and coastal waters during their first summer. Like many fishes along the mid-Atlantic coast, weakfish move offshore to overwinter as coastal waters cool during the fall, returning in the spring when inshore temperatures increase.

The seasonal inshore and offshore movements of weakfish could lead to significant mixing of fish from different coastal areas. Tagging studies by Nesbit (1954) showed that a large proportion of weakfish tend to return to the same coastal region in which they were tagged, although many fish were recaptured in areas distant from the original tagging location. The differential size distribution of weakfish along the mid-Atlantic coast is consistent with the hypothesis that mixing of weakfish from different coastal areas occurs. Larger (older) weakfish are more predominant in northern waters during the summer, and the mean size of weakfish tends to decrease as one moves down the Atlantic coast (Wilk and Silverman 1976). Whether this represents an ontogenetic change in seasonal movements or differential survival or growth of fish from different coastal areas is not known.

Weakfish support an important commercial and recreational fishery. Commercial landings over the past 110 years have undergone dramatic fluctuations. Combined commercial and recreational landings were at a recent peak during 1980 at 36,400 metric tons (t) and subsequently dropped to about 19.1 t over a period of 2 years (Vaughan et al. 1991). The total catch has remained fairly constant for the last 8 years, although a significant decline in landings from northern waters has been noted over the period (Vaughan et al. 1991). For example, the combined commercial

* Contribution 1749 of the Virginia Institute of Marine Science and School of Marine Science, College of William and Mary.

and recreational catch in New York dropped from 840t in 1982, to 224t in 1986, to 10t in 1990 (NMFS Current Fishery Statistics Series). The recreational catch typically represents a sizable fraction of the total landings, and at times surpasses the commercial catch (Wilk 1979).

Many weakfish are lost from the fishery as incidental bycatch in shrimp trawling operations. The incidental weakfish bycatch, which is greatest in the southern part of the species' range, consists mostly of young-of-the-year fish. It is difficult to determine the magnitude of the weakfish bycatch, but it is estimated that it exceeds the combined recreational and commercial catch in the southern states (South Carolina, Georgia and Florida) and may approach 30% of the total coastal fishery for adults (Keiser 1976, Mercer 1983, Vaughan et al. 1991).

The Fishery Management Plan for Weakfish was adopted in 1985 by the Atlantic States Marine Fisheries Commission (Mercer 1985). At that time, the genetic basis of weakfish stock structure was not well understood, and most states have independently managed their weakfish fisheries. As a result, different gear restrictions and minimum sizes are enforced along the mid-Atlantic coast. For example, Florida, Georgia, South Carolina, North Carolina, New Jersey, and Connecticut have no recreational minimum size limit, but a 9-inch size limit is enforced in Virginia, 10 inches in Maryland and Delaware, and 12 inches in New York and Rhode Island.

A thorough understanding of weakfish stock structure is essential for effective management of the fishery. Several management decisions require knowledge of the interdependence of fishery resources from different coastal areas. The recent decline in landings from northern waters has coincided with increased catches of large weakfish in the North Carolina winter offshore (sinknet) fishery (Vaughan et al. 1991), but it is not known if the two fisheries operate on the same stock of fish. On a larger geographic scale, the relationship between bycatch mortality of young weakfish in southern waters and landings of older weakfish in northern waters in subsequent years has not been determined. A detailed genetic analysis of weakfish stock structure would provide information required to test hypotheses of the independence of weakfish from different coastal areas.

Several studies have investigated weakfish stock structure employing a variety of ecological and morphological techniques including mark and recapture data (Nesbit 1954), scale circuli patterns (Perlmutter et al. 1956), morphological characters (Seguin 1960, Scoles 1990), and relative growth rates and reproductive characters (Shepherd and Grimes 1983, 1984). Most of these studies concluded that weakfish comprise two or more stocks; however, the inability to distinguish between ecophenotypic and genetic character variation in these studies has confounded interpretation of the results.

There are few studies on the biochemical genetics of the weakfish. Crawford et al. (1989) analyzed water-soluble protein variation using starch gel electrophoresis. They found no significant genetic differentiation between weakfish collected from Buzzards Bay MA to Cape Hatteras NC, and so were unable to disprove the null hypothesis that weakfish along the mid-Atlantic coast share a common gene pool. Of the 25 protein-encoding loci surveyed in the Crawford et al. (1989) study, only two were polymorphic within the pooled sample, and the mean heterozygosity was low relative to other marine fishes.

Studies of protein variation have been extremely useful in demonstrating the intraspecific genetic structure of many marine fishes (reviewed in Ryman and Utter 1987). For those species which display little intraspecific variation, like the weakfish, sample sizes must be very large to detect significant differentiation between putative stocks, if it exists. In such cases, analysis of a more rapidly evolving set of molecular characters may provide a better estimate of population structure with a more manageable number of samples. Restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA) has provided such a tool, and the technique has been useful in resolving stock structure within species which exhibit little protein variation (reviewed by Ovenden 1990).

This paper reports the results of an RFLP analysis of weakfish mtDNA to determine if fish along the mid-Atlantic coast share a common gene pool. The study began as a spatial and temporal investigation of a large number of individuals from a few collection sites along the central mid-Atlantic coast with 6 restriction endonucleases. Because there was a high degree of genetic homogeneity among these samples, we expanded the investigation to include an intensive analysis of weakfish from the northern and southern ends of the species' range with 13 restriction endonucleases.

Materials and methods

For our sampling protocol we assumed that if separate genetic stocks of weakfish exist, they should be separated at the time of spawning. We therefore restricted our collections to female weakfish that were ready to spawn as evidenced by high gonadosomatic indices (GSI). For example, the mean GSI of the New York 1988 sample was 7.7% ± 3.1SD.

Ripe, female weakfish were obtained from commercial fishermen, sportfishing tournaments, and the

National Marine Fisheries Service Inshore Trawl Survey. Dates and locations of capture, and the size composition of the collections are presented in Table 1. Freshly-caught weakfish were measured for standard length and then dissected. Ovaries were removed and quickly frozen at −20°C.

Mitochondrial DNA was obtained by the rapid isolation procedure of Chapman and Powers (1984) for the initial survey of mtDNA genetic heterogeneity. After ethanol precipitation, the mtDNA-enriched DNA pellet was rehydrated in 75 μL of distilled water, and the yield from ~7 g of ovarian tissue was usually sufficient for at least 7 restriction digestions visualized with ethidium bromide.

The 1988 and 1989 samples were surveyed with the following six restriction endonucleases: *Ava*I, *Bam*HI, *Bgl*I, *Hind*III, *Nci*I, and *Pvu*II. Restriction fragments were separated by horizontal gel electrophoresis on 0.8–1.5% agarose gels run at 2 v/cm for 16 h. Gels of restriction digestions of isolations containing high yields of mtDNA were visualized after ethidium bromide staining with ultraviolet light illumination (Maniatis et al. 1982) and photographed with a Polaroid CU-5 camera using a Wratten #5 filter. For those samples in which there was not sufficient mtDNA for direct visualization, restriction digestions were endlabeled before electrophoresis with the appropriate ^{35}S nucleotide triphosphate using the Klenow fragment (Maniatis et al. 1982). After electrophoresis, the gels were rinsed with a scintillation enhancer, dried, and autoradiographed at −70°C for 5 d.

To compare the genetic relationship of weakfish from the northern and southern ends of their range in greater detail, mtDNA was purified from ovarian tissues using the CsCl density-gradient centrifugation protocol of Lansman et al. (1981). The mtDNA from these samples was surveyed with the 6 restriction endonucleases listed above and the following 7 enzymes: *Apa*I, *Ava*II, *Ban*I, *Bcl*I, *Eco*RV, *Hinc*II, and *Hha*I. The restriction digestions were endlabeled, separated on agarose gels, and autoradiographed as described above.

The different fragment patterns produced by each restriction endonuclease were each assigned a letter. A composite mtDNA genotype, consisting of the letters representing the fragment patterns generated by each restriction endonuclease, was then constructed for each individual. The nucleon diversity (Nei 1987) was calculated for each sample and for the pooled samples. The percent nucleotide sequence divergence between mtDNA genotypes was estimated by the site approach of Nei and Li (1979) and the percent mean nucleotide sequence divergences within and among weakfish samples were calculated following the method of Nei (1987), with the latter value being corrected for within-group heterogeneity. The distribution of genotypic frequencies was evaluated for homogeneity between collections using the G-test (Sokal and Rohlf 1981).

Table 1
Weakfish *Cynoscion regalis* collection data.

Sample	Location	Date	*N*	Standard length Mean, range (mm)
NY88	Long Island NY	6/88	58	560, 254–750
NY89	Long Island NY	5/89	65	619, 216–750
DE88	Lewes DE	5/88	74	597, 256–761
DE89	Lewes DE	5/89	51	521, 290–744
DE91	Lewes DE	6/91	25	522, 390–670
NC88	Hatteras NC	6/88	72	278, 221–342
SO91	SC, GA, FL	5/91	25	201, 174–273

Table 2
Distribution of weakfish *Cynoscion regalis* mtDNA genotypes based on 6 restriction endonucleases among the different collections. The order of restriction enzyme morphs, represented from left to right, is *Hind*III, *Pvu*II, *Bgl*I, *Bam*HI, *Nci*I, and *Ava*I. Fragment sizes for each restriction pattern are available from the senior author upon request.

	Sample							
Genotype	NY88	NY89	DE88	DE89	DE91	NC88	SO91	Total
AAAAAA	55	60	67	48	22	69	24	345
AAAAAC	0	2	2	0	1	1	0	6
AAAAAB	0	0	2	0	1	0	1	4
AAAAFA	1	0	0	1	0	1	0	3
AAAADA	0	2	0	1	0	0	0	3
ABAAAA	1	1	0	0	0	0	0	2
AAAABA	1	0	1	0	0	0	0	2
AAAACA	0	0	2	0	0	0	0	2
DAAAAB	0	1	0	0	0	0	0	1
AAAAEA	0	0	0	0	0	1	0	1
CAAAAA	0	0	0	0	0	1	0	1
Total	58	66	74	50	24	73	25	370

Results

Weakfish mtDNA demonstrated very little variation. Of the 370 weakfish surveyed with 6 restriction endonucleases, 345 shared a common mtDNA genotype (Table 2). Ten variant genotypes were encountered in

the analysis, distributed among the remaining 25 individuals. In each case, variant genotypes were closely related to the common genotype, differing by no more than two restriction site changes. Restriction site gains or losses were inferred from completely additive changes in fragment patterns. No length polymorphisms or heteroplasmy were observed. A total of 43 restriction sites were detected in the 6-enzyme survey, and the average individual was scored for 29 sites, representing about 1.0% of the weakfish mtDNA genome.

The common mtDNA genotype, AAAAAA, occurred in the great majority of fish in all samples, ranging in frequency from 0.905 (DE88) to 0.960 (DE89, SO91), with a value of 0.932 for the pooled sample (Table 2). The next most-common genotype, AAAAAC, occurred in the pooled sample at a frequency of 0.017, and was present in 4 of the 7 samples. Because of the predominance of a single genotype in all samples, nucleon diversities were relatively low (Table 3), ranging from 0.079 (DE89) to 0.180 (DE88), with a value of 0.130 for the pooled samples. As all variant mtDNA genotypes were related to the common genotype by no more than 2 restriction site changes, the percent mean nucleotide diversity within each sample was also quite low (Table 3), ranging from 0.06 (DE89) to 0.18 (NY89).

Little genetic differentiation was detected among weakfish samples collected at the same location over 2 or more years (Table 4). Among samples collected in Delaware during 1988, 1989, and 1991, and in New York during 1988 and 1989, the percent mean nucleotide sequence divergences, corrected for within-sample variation (Nei 1987), ranged from 0.00 (DE88/DE91, NY88/NY89) to 0.01 (DE89/DE91).

Little genetic differentiation was encountered among samples of weakfish collected along the mid-Atlantic coast. The nucleotide sequence divergences among samples collected at geographically distant sites during the same spawning season ranged from 0.00 (NY88/NC88) to 0.03 (NY89/DE89). These values are of the same magnitude as those found among samples of weakfish collected at the same site over 2 or more years, indicating a lack of spatial genetic structuring.

An analysis of the distribution of mtDNA genotypes also revealed no significant heterogeneity among temporal or spatial collections. To avoid a bias caused by including expected values <1, we initially pooled all alternate genotypes for an analysis of heterogeneity. The results of a G-test (Sokal and Rohlf 1981) revealed no significant spatial or temporal differences in the distribution of the common and pooled rare genotypes among the 7 samples (G_H 2.88, $0.75>p>0.50$). Expanding the analysis to include the common genotype and all 10 rare genotypes separately (each with expected values <1 in one or more collections) did not significantly change the outcome. Once again, the null hypothesis of homogeneity could not be disproved (G_H 51.62, $0.50>p>0.25$).

Table 3

Genotypic diversity and percent mean nucleotide sequence diversities for 7 weakfish *Cynoscion regalis* collections. Values for both 6 and 13 restriction enzyme surveys are listed for the Delaware (DE) 1991 and southern (SO) 1991 samples.

Sample		Nucleon diversity	Percent mean nucleotide sequence diversity
NY88		0.102	0.09
NY89		0.171	0.18
DE88		0.180	0.15
DE89		0.079	0.06
DE91	(6)	0.163	0.19
	(13)	0.239	0.10
NC88		0.107	0.11
SO91	(6)	0.080	0.09
	(13)	0.080	0.04
Total		0.130	0.13

Table 4

Percent mean nucleotide sequence divergences between weakfish *Cynoscion regalis* collections. Values are based on results from 6 restriction endonucleases and have been corrected for within-group sequence diversity (Nei 1987).

	NY89	DE88	DE89	DE91	NC88	SO91
NY88	0.00	0.00	0.00	0.01	0.00	0.00
NY89	—	0.00	0.03	0.00	0.00	0.00
DE88	—	—	0.00	0.00	0.00	0.00
DE89	—	—	—	0.01	0.02	0.00
DE91	—	—	—	—	0.00	0.00
NC88	—	—	—	—	—	0.00

The low level of variation detected in our analysis of weakfish mtDNA could be the result of many factors. After reviewing the 1988 and 1989 results, we felt that we might have biased our estimates of mean nucleotide sequence divergence by using 6 restriction endonucleases that, by chance, were not variable within weakfish. To test this hypothesis, we analyzed the DE91 and SO91 weakfish collections with an additional 7 restriction endonucleases. The average individual in the 13-enzyme analysis was scored for 65 restriction sites, or approximately 2.4% of the weakfish mtDNA molecule. Of the 49 fish in the two samples surveyed, only one variant mtDNA genotype was found (one fish from the SO91 sample with the common 6-enzyme mtDNA genotype exhibited a site gain relative to the common pattern for the enzyme *Bcl*I). As a result,

the nucleon diversity, which is sensitive to the number of enzymes employed, increased for only one of the two samples. The within-sample percent mean nucleotide sequence diversity, which is not as sensitive to the number of restriction sites surveyed, was slightly lower for both samples (Table 4), and the corrected values of percent mean nucleotide sequence divergence between the DE91 and SO91 samples was essentially the same whether based on 6 or 13 informative restriction enzymes.

Discussion

The presence of alleles unique to samples from particular geographic locations has been used to infer intraspecific genetic structuring and to determine levels of gene flow among collection sites (Slatkin 1989). This model assumes that increased frequencies of "private" alleles are a direct result of limited gene flow. An inspection of the above data reveals several genotypes that are present at very low frequencies (Table 2); however, it is interesting to note that most genotypes represented by more than a single individual occur in two or more geographic samples. For example, the genotype AAAAFA was encountered three times in the analysis of 370 weakfish, occurring in the NY88, NC88, and DE89 samples. The lack of spatial partitioning of rare alleles is strongly suggestive of a high rate of gene flow among collection locations.

The level of mtDNA variation found within the weakfish is among the lowest reported for any species of fish. While it is difficult to compare nucleon diversities from different studies because the value is dependent upon the number of restriction sites surveyed, relative levels of variability can be determined from comparisons of studies involving about the same numbers and types of restriction endonucleases. The nucleon diversity of the 1991 weakfish samples surveyed with 13 enzymes was 0.157, a value that falls well below the range of 0.473–0.998 reported by Avise et al. (1989) for other fishes analyzed with about the same number of enzymes. The nucleon diversity of the weakfish was also substantially below the mean value of 0.943 reported for the red drum *Sciaenops ocellatus* (Gold and Richardson 1991). Relatively low values of nucleon diversity have been found for the black drum *Pogonias cromis* (0.584) and the spotted seatrout *Cynoscion nebulosus* (0.531), a congener of the weakfish (C. Furman and J.R. Gold, Texas A&M Univ., College Station, pers. commun., Aug. 1991). However, these values are still substantially larger than those we found for the weakfish. Comparisons of nucleotide sequence diversities among these species also indicate that the weakfish is relatively depauperate in terms of mtDNA variation. The mean percent nucleotide sequence diversities within 7 black drum samples (0.142) and 5 spotted seatrout samples (0.222) are substantially higher than that within the 7 weakfish samples (0.10) surveyed in this study.

The finding of relatively low levels of mtDNA variation within the weakfish is consistent with the lack of allozyme variation reported by Crawford et al. (1989). Low levels of mtDNA variation have generally been attributed to small effective population sizes of females, resulting in relatively rapid sorting of gene trees (Nei 1987, Avise et al. 1988, Chapman 1990, Bowen and Avise 1990). Variations in weakfish abundance over the last 110 years have been reflected in commercial catches, which have fluctuated from a high of 44.5 million pounds in 1908 to a low of 3.1 million pounds in 1967 (Vaughan et al. 1991), but it is unlikely that such variations over recent history have drastically reduced the effective population size of female weakfish. Population bottlenecks on a larger time-scale (e.g., glaciation events) or cyclical fluctuations in population size may have resulted in the reduced genetic diversity within the weakfish, but such explanations are merely speculative and do not necessarily agree with the observation that other sciaenids with similar distributions and life histories do not exhibit such low levels of mtDNA diversity.

Reductions in effective population size can also occur due to differential reproductive contribution, resulting from skewed sex ratios, limited mating opportunities, or varying of survival among progeny. While little is known of weakfish spawning behavior or differential recruitment success, the sex ratio tends to be very close to 1.0 (Wilk 1979). Thus, the cause or causes contributing to the low genetic variation observed among weakfish relative to other fishes is problematic.

In addition to low levels of within-sample variation, we detected little temporal or spatial genetic differentiation among weakfish samples. Because there were few variant mtDNA genotypes, and almost all of the rare variant genotypes occurred in more than one population, the uncorrected mean nucleotide sequence divergences among weakfish samples were of the same magnitude as mean nucleotide diversities found within samples. Thus, the mean difference among mtDNA genotypes randomly drawn from within a single sample was equivalent to the mean difference among mtDNA genotypes drawn from different samples.

Low levels of within-group mtDNA variation do not preclude the occurrence of significant between-group differentiation. Bowen and Avise (1990) recently reported low values of mtDNA diversity within samples of Atlantic and Gulf of Mexico black sea bass *Centropristis striata* (within-sample percent nucleotide sequence diversity of 0.03), yet their study revealed

significant differentiation between the two populations (an uncorrected percent mean sequence divergence of 0.75). The lack of significant population structuring within the weakfish relative to the black sea bass is evidenced in a comparison of the ratio of between-group to within-group sequence divergences: For the black sea bass the ratio is 24, while for the weakfish it is ~1.

The results of our investigation suggest that weakfish comprise a single genetic stock throughout the species' range. No significant genetic differentiation was found among geographic samples or among samples taken at the same site over several years. Consequently, at the level of genetic resolution we employed, we cannot disprove the null hypothesis that weakfish share a common gene pool. The inference that gene flow occurs throughout the species' range is supported by the homogeneous distribution of rare mtDNA genotypes.

The genetic homogeneity found within the weakfish in this study and in the allozyme analysis of Crawford et al. (1989) contrast with the geographical variation of morphological and life-history characters reported in other studies (Perlmutter et al. 1956, Seguin 1960, Shepherd and Grimes 1983 and 1984, Scoles 1990). The degree of plasticity of weakfish morphological and life-history characters to different environmental conditions has not been determined, but in light of research on other fishes (Barlow 1961), it would not be surprising if much of the geographic variation previously described among weakfish is ecophenotypic.

Our inference that there is sufficient gene flow among weakfish along the mid-Atlantic coast to prevent even minor genetic differentiation from occurring has several management implications. There is clearly some interdependence among areas, a conclusion also supported by the tagging data of Nesbit (1954). To obtain a meaningful estimate of the magnitude of the interdependence between these areas would require a tagging study much more extensive than that of Nesbit (1954), which would involve considerable time and expense. Until such information is available, it would be best to manage the weakfish resource conservatively, as a single interdependent stock.

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An assessment of the exploitable biomass of *Heterocarpus laevigatus* in the main Hawaiian Islands. Part 2: Observations from a submersible

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Abstract. – Five submersible dives were conducted to evaluate the behavior of deepwater shrimp and the relationship of their density to bottom type and trap yield. Differences in behavior of two species of *Heterocarpus* were observed: *H. ensifer* tended to group around large anemones and other benthic relief over otherwise flat, sandy bottom and were very active in the presence of a baited container; whereas *H. laevigatus* were solitary and showed little activity around a baited container. Greater densities of *H. laevigatus* were observed on volcanic than on coralline substrate, indicating a possible association with this bottom type. Trap catches were regressed against observed *H. laevigatus* densities yielding an estimate of the catchability coefficient. This coefficient differed from that obtained from a previously conducted Leslie model depletion study. Factors contributing to this difference may include comparing estimates of catchability based on data from different areas, bias in the estimate of catchability based on observed density, and bias in the estimate of catchability from the depletion study. A combined fishing and visual census study is suggested as the best assessment technique.

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Tropical deepwater pandalid shrimp have potential for commercial harvesting in many areas of the Pacific (Struhsaker and Aasted 1974, Wilder 1977, Moffitt 1983, King 1984, Tagami and Barrows 1988). These shrimp are readily trapped but not easily trawled (Struhsaker and Aasted 1974). The largest and most commercially desirable species in Hawaii is *Heterocarpus laevigatus* (Tagami and Barrows 1988); the smaller *H. ensifer* has less commercial appeal but is also abundant (Struhsaker and Aasted 1974). In the early 1980s, several boats initiated a trap fishery targeting *H. laevigatus*, and landings rose to a high of 159 metric tons (t) in 1984 (HDLNR 1986). By 1985, most vessels left the fishery, and the annual landings dropped to <6 t/yr (West. Pac. Fish. Inf. Network, NMFS Honolulu Lab., unpubl. data).

Early predictions of maximum sustainable yield for Hawaiian shrimp, based on little or no direct data, were as much as 1000–2000 t/yr (Struhsaker and Aasted 1974, HDLNR 1979). Recent research on population dynamics combined with systematic trapping surveys has resulted in more refined estimates of exploitable biomass and maximum sustainable yield for *H. laevigatus* in various island locations (Dailey and Ralston 1986, Ralston 1986, Moffitt and Polovina 1987, Ralston and Tagami 1992). The most recent estimate of exploitable biomass for the main Hawaiian Islands, 271–1050 t, is based on an estimate of the catchability coefficient (q) obtained through a Leslie model depletion study, coupled with catch-per-unit-effort (CPUE) values and habitat area estimates obtained through systematic trapping (Ralston and Tagami 1992).

The relationship of observed target-species density to fishing-gear CPUE has been used to estimate stock biomass and catchability (Ralston et al. 1986, Kulbicki 1988). Estimates of abundance obtained through visual census techniques are generally higher than those based on catches of fishing gear, and the relative reliability of the various assessment methods must be analyzed on a case-by-case basis (Uzmann et al. 1977, Powles and Barans 1980, Kulbicki and Wantiez 1990, Matlock et al. 1991).

In the present study, we conducted submersible dives at several sites in the Hawaiian Islands to observe shrimp behavior both away from and in the vicinity of a baited container and to record density and substrate associations of *H. laevigatus*. Observations of shrimp behavior and substrate associations have applications to commercial fishermen in terms of

trapping technique and site selection. The mean of observed densities recorded during submersible dives is regressed against yields of a trap set at the dive sites to obtain an estimate of q, and this value is compared with that reported by Ralston and Tagami (1992). An accurate estimate of catchability is important in order to better estimate exploitable biomass for management purposes.

Methods

A total of five submersible dives were conducted in the main Hawaiian Islands, at two sites off leeward Oahu in February 1988 and three sites off the Kona coast of the Island of Hawaii in August 1988 (Table 1). The Oahu sites were selected for their proximity to port and because of previously-observed concentrations in the area of unidentified red shrimp at appropriate depths (400–900 m) for *Heterocarpus*. The three Kona sites were selected as extremes in *H. laevigatus* yield for the area during a trapping survey using pyramid traps conducted in March 1988 (see Tagami and Barrows (1988) and Ralston and Tagami (1992) for trap description and trapping methods). Catches of *H. laevigatus* were lowest for the Kona area (<1 kg/trap-night) at one of the sites and highest (>10 kg/trap-night) at the remaining two sites.

Visual censuses

All dives used the *Pisces V*, a three-man submersible that allowed simultaneous observations by two researchers through separate view ports with non-overlapping fields of view directed diagonally forward and down. A video camera continuously recorded the bottom throughout each dive as well. The same two researchers estimated shrimp abundance on all dives and independently reviewed the dive video tapes as a check on observer bias. On each survey, the submersible descended to depths of 480–920 m, then traveled to an arbitrary starting location at ~600–750 m depth. At this point, a baited container was placed on the bottom and observations of shrimp behavior in the presence of bait were recorded. After observing shrimp behavior for ~15 min, the submersible traveled a haphazard, rectangular track at a speed of ~2 knots along the contours within the zone of maximum shrimp abundance (defined below), returning to the baited container for retrieval at the end of the dive. At preselected time-intervals (5 or 10 min), the submersible settled to the bottom and counts of shrimp were taken by each observer in an independent quadrant filling the field of view. The estimated area of each quadrant was 10 m^2, which was calibrated by underwater observation of known dimensions with the submersible attached to its launch-and-retrieval vehicle. The minimum distance between observation sites was ~100 m. The number of observations of shrimp density varied between dives, for bottom time was dependent on battery power.

Table 1
Locations of five study sites off the islands of Oahu and Hawaii and 1988 sampling dates.

Site no.	Location	Dive date	Trap date
Oahu			
1	21°19.3′N, 158°10.1′W	8 Feb.	13 Mar.
2	21°31.0′N, 158°16.8′W	9 Feb.	13 Mar.
Kona			
1	19°14.0′N, 155°54.9′W	23 Aug.	18 Mar.
2	19°20.7′N, 155°54.2′W	24 Aug.	18 Mar.
3	19°47.5′N, 156°07.8′W	25 Aug.	15 Mar.

Bottom depth, temperature, and substrate type were recorded with each shrimp count. The substrate within each quadrant was categorized by composition and particle size of the major component. Substrate composition included coralline, volcanic, and mixed; particle size included sand, rock both small (~<15 cm diameter) and large (>15 cm diameter), and pavement.

A χ^2 goodness-of-fit test using a Poisson distribution for the expected frequencies was conducted to determine whether *H. laevigatus* were concentrated or evenly distributed over the bottom at each dive site. Mean *H. laevigatus* density and 95% CI was calculated for each dive site based on a Poisson distribution,

$$CL = D_{(i)} \pm (1.96)\left(\frac{(D_{(i)}}{n_{(i)}}\right)^{1/2},$$

where $D_{(i)}$ and $n_{(i)}$ are the mean density and number of observations for each dive site. Expected density values (De) for each site were calculated using trap landings for the site and the normalized catchability coefficient (q) reported by Ralston and Tagami (1992), using the following formula:

$$De_{(i)} = \frac{CPUE_{(i)}}{q}.$$

Confidence limits for the expected density values for each site could not be calculated, since variance cannot be computed for CPUE, based as it is on the catch of a single trap.

An analysis of variance (ANOVA) was performed to determine whether higher mean densities of *H. laevi-*

gatus could be attributed to different dive sites or bottom types and to determine whether there was observer bias. Independent variables for the ANOVA were dive site, substrate material, substrate particle size, and observer.

Comparisons of trap landings and density estimates

Trap catch rates were obtained in March 1988 from one pyramid shrimp trap set at each of the five dive sites and allowed to soak overnight (see Ralston and Tagami (1992) for details). Trap catches of *H. laevigatus* were regressed against mean densities obtained from visual counts for the five study sites, fitting a linear model with a zero intercept. The slope of this regression is an estimate of q, which was compared with that reported by Ralston and Tagami (1992).

Results

A total of 923 shrimp were captured in the 5 pyramid traps set at the study sites. Of these, 705 (76%) were *H. laevigatus* (Table 2), 217 were *H. ensifer*, and 1 was *Acanthephyra eximia*. During the scheduled observation periods on the submersible dives, a total of 494 shrimp were observed (194 total quadrant observations). Of these, only 95 (19%) were *H. laevigatus*, and the remainder consisted primarily of *Plesionika* sp., tentatively identified as *P. ensis*, and a few individuals of *P. alcocki*, *H. ensifer*, *A. eximia*, and *Gnathophausia longispina*. All *H. laevigatus* observed from the submersible appeared well within the size range of those captured in the traps, indicating that both stock assessment methods sample the same population.

Visual censuses

During our dives, the shrimp showed little reaction to the presence of the submersible or its lights. When the submersible came within a few inches of the shrimp, they swam a short distance avoiding collision. When the photoflash was used, the shrimp within a few feet of the submersible started, darting a distance of 1–4 cm. No other reactions to the submersible or its lights were observed. Several behavioral differences were noted between the various species observed.

A total of 94% (89 of 95) of the *H. laevigatus* observed during census periods were seen between 550 and 675 m, the depth range herein defined as the zone of maximum abundance. Individuals of *H. laevigatus* were observed at each dive site, but not necessarily during the scheduled census periods conducted within the zone of maximum abundance. Only counts taken within this depth range were used in the analysis.

Table 2

Trap catches, predicted densities, and mean observed densities with 95% CL of *Heterocarpus laevigatus* at five study sites off the islands of Oahu and Hawaii in 1988. N = the number of observations.

Dive site	Trap catch (*n*/trap)	Density (*n*/ha)			
		Predicted	Observed	CL	N
Oahu					
1	5	0.53	0	—	34
2	26	2.7	0	—	8
Kona					
1	0	0	200	(−680)–1080	10
2	376	40	1360	(−570)–3290	14
3	298	31	890	220–1560	76

Heterocarpus laevigatus were observed as solitary individuals on the bottom, usually stationary but occasionally walking, and rarely swimming near the bottom. They showed little activity in the presence of a baited container and were not observed crawling over or entering it. Conversely, *H. ensifer* were found in groups near relief features (e.g., large sea anemones) at shallower (450–550 m) depths, either stationary on the bottom or swimming about 1 m above the bottom. They were very active in the presence of a baited container, aggregating quickly and crawling over and entering the container through the mesh and other holes. *Plesionika alcocki* usually were seen on the bottom, whereas *P. ensis* generally were seen hanging motionless in the water column ~1–2 m off the bottom. Each showed some activity around the baited container. *Acanthephyra eximia* and *G. longispina* were observed swimming 1–2 m off the bottom, but were not seen at the baited container.

Bottom temperature varied during the dives from a low of 3.9°C at 920 m to a high of 6.0°C at 480 m. The temperature range within the zone of maximum *H. laevigatus* abundance was 4.8–5.9°C.

Bottom type varied considerably among the sites. The bottom at the two Oahu sites was classified as coralline sand making up an even, featureless plain with a gradual (<20°) slope. The bottom at the three Kona coast sites was much steeper, generally about a 35–45° slope, but with some sections near vertical or even slightly undercut at the Kona site 3. At Kona site 1, the bottom was nearly uniformly composed of small (5–10 cm diameter), sharp-edged volcanic rocks and very little coralline material. Kona site 2 differed from site 1 in that the small volcanic rocks were more weathered and the substrate had a greater coralline component. Kona site 3 had many sandy areas, at

Table 3
Analysis of variance for *Heterocarpus laevigatus* density by dive, bottom type, and observer.

Source	df	SS	MS	F	P
Dive	4	31.25	7.81	6.87	0.0001
Substrate material	2	24.53	12.26	10.79	0.0001
particle size	3	5.96	2.98	2.62	0.0765
Observer	1	3.40	3.40	2.99	0.0859
Error	132	150.08	1.14	—	—
Corrected total	141	215.22	—	—	—

times covering the entire 10 m^2 quadrant, as well as areas of exposed limestone often forming undercut cliffs, and areas of small weathered volcanic rocks.

The distribution of *H. laevigatus* over the bottom was evaluated in several ways. No significant values were found for the χ^2 goodness-of-fit tests ($P>0.10$) of the density observations recorded at each dive site, suggesting that the shrimp were randomly distributed (in a Poisson manner) instead of clumped at each dive site. The mean and confidence intervals of *H. laevigatus* density observed at each dive site are presented in Table 2. Pooling data from all dive sites for the independent variables (dive site, substrate material, substrate particle size, and observer), only dive site and substrate material were significantly correlated with shrimp density (ANOVA, $P<0.05$; Table 3). The distribution of residuals did not differ significantly from a normal distribution. Independent review of the dive video by each observer yielded complete agreement on *H. laevigatus* counts and substrate classification, indicating a lack of observer bias in shrimp density estimation and substrate associations.

Comparisons of trap landings and density estimates

Mean observed densities were regressed on trap catches for each dive site (Fig. 1) (r^2 0.97, P 0.0003). The least-squares regression equation is

$$CPUE_i = 0.2896\ (D_i), \qquad (SE\ 0.02364).$$

An estimate of catchability is obtained directly from the value of the slope (0.2896 ha/trap-night) with a confidence interval calculated as 0.2144–0.3648/trap-night. This estimate of catchability is <1/30th that reported by Ralston and Tagami (1992) and is reflected in the differences between observed and expected *H. laevigatus* densities for Kona sites 2 and 3 (Table 2).

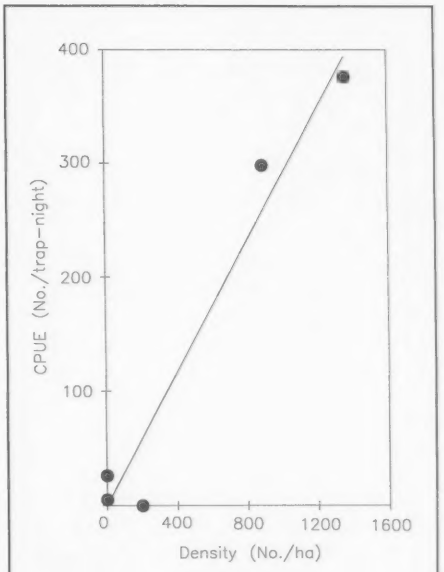

Figure 1
Regression of trap catch per unit effort (CPUE; number per trap-night) and observed density of *Heterocarpus laevigatus* (number/hectare) at five sites in the Hawaiian Islands.

Discussion

Differences in behavior between *H. laevigatus* and *H. ensifer*, the two species with greatest commercial potential, may lead to some practical applications for fishermen. The high activity level noted for *H. ensifer* in the presence of a baited container has also been reported by Gooding et al. (1988) and Saunders and Hastie (1989). The rapid attraction and entry of this species into traps, even during daylight hours, indicate that a short soak time may be adequate for commercial harvesting. The lower activity level of *H. laevigatus* observed in our study and reported by Saunders and Hastie (1989) may indicate that a longer soak time is more appropriate for this species. If so, a small vessel with a limited number of traps could maximize total catch by making two short sets during daylight hours on *H. ensifer* grounds, followed by an overnight set on *H. laevigatus* grounds, assuming that suitable concentrations of both species are present within a reasonable proximity.

Previous observations of *H. ensifer* from a submersible found higher densities on flat, silty, sandy areas than over low-relief, rocky outcroppings (Gooding et al. 1988). Although statistical analysis of substrate associations were not conducted for *H. ensifer* in this study, we did observe a similar substrate association. *Heterocarpus ensifer* were abundant at the Oahu dive sites at depths (500–800 m), although this is deeper than their reported optimum range of 300–600 m (Gooding 1984). The substrate on these two dives was flat, coralline sand with few isolated, low-profile features (e.g., sea anemones, small rocks) around which the shrimp appeared to concentrate. No rocky outcroppings were observed on these dives. Very few *H. ensifer* were observed at the three Kona dive sites, where the bottom was steep and composed largely of rocky rubble with few sandy patches, though the dive depths again were deeper than the optimum range for this species.

The substrate associations of *H. laevigatus* appeared to differ from those of *H. ensifer*. Although the differences in substrate particle size were not significant, the ANOVA test revealed significantly higher densities on volcanic compared with coralline substrates (Table 3) with data from all dive sites pooled. The significant results for substrate type, however, must be viewed with caution because of the significance of dive site to *H. laevigatus* density and the unbalanced sample design. Not only were all substrate types not present on a single dive, but those types present were not found in equal proportions on any dive. Therefore, differences in density attributed to substrate type may actually be a reflection of differences related by some other factor to dive site. In particular, the Kona dive sites were largely volcanic, and the majority of the *H. laevigatus* observed were from Kona sites 2 and 3. Although Kona site 1 also was largely volcanic, the volcanic rocks differed from those observed at sites 2 and 3, in that the appearance was of a more recent rock slide (sharper edges vs. weathered). This apparent instability may be responsible for the low shrimp density observed at site 1. Other aspects of the bottom, such as slope, substrate complexity, stability, and current patterns may be of considerable importance and should be investigated in future work on the substrate associations of *H. laevigatus*.

With visual censusing techniques, there is always a concern regarding the reliability of abundance estimates. Various factors, including sampling techniques, species behavior, and physical conditions, can bias results (Colton and Alevizon 1981, Sale and Douglas 1981, Brock 1982, Ralston et al. 1986, Matlock et al. 1991). Some authors believe that density estimates based on direct visual surveys, though often much higher, are more reliable than those estimated from fishing gear catches (Uzmann et al. 1977, Powles and Barans 1980, Kulbicki and Wantiez 1990). Individuals of the target species, *H. laevigatus*, were easily counted because they were in the open and reacted almost with indifference to the presence of the submersible, and because the low, uncomplicated relief at the study sites offered little opportunity for their concealment. Avoidance of the submersible by the shrimp seems unlikely. Observed densities were much greater than expected, yet these would be underestimates if avoidance occurred. We cannot discount the possibility of bias in our density estimates caused by attraction of shrimp to the baited container placed at the beginning of our dives. However, we observed no increased density gradient in the vicinity of the container, and density observations were taken well away from the container site (>100 m), presumably outside the drawing range of the bait, leading us to believe that bias due to this source was small.

Recalculation of exploitable biomass for the main Hawaiian Islands using Ralston and Tagami (1992) data and methods, but substituting the q value obtained in this study, would lead to a 33-fold increase in the estimate of exploitable biomass (~9000 t instead of 271 t). Just as Ralston and Tagami (1992) suggest that their estimate may be too low, we suggest that 9000 t may be unreasonably high, considering the preliminary nature of this estimate and the failure of the Hawaiian fishery that was at least partly due to drops in catch rates at annual yields of <200 t (Tagami and Barrows 1988). The acceptance of either of these estimates would drastically affect management decisions, and careful evaluation of these two values must be made. Contributions to the difference between the two estimates may be from three sources: actual differences in catchability for the two studies related to differences in time and study locations, error in our estimate of q, and error in the Ralston and Tagami (1992) estimate.

The estimation of q can be influenced by a variety of factors including currents, water turbidity and temperature, type of bait, soak time of fishing gear, and density of the target species (Morgan 1974, Richards and Schnute 1986, Miller 1990). For the two studies involved in this discussion, many of the potential sources of error were standardized. Both studies used the same traps, same bait, and same soak times. They did not, however, conduct studies at the same location or time, and the range of catch rates encountered differed for the two studies. In both studies it is assumed that catchability is constant for all catch rates and densities involved, but this may not be true, particularly between studies. Unfortunately, we are unable to evaluate the extent of the error involved from these sources.

The estimate of q presented in this study could also be biased. Sources of potential bias include lack of

representative catch rates for study sites, error in density estimation, incompatibility of CPUE and density estimates collected at different points in time, and the few data pairs involved. Not only were shrimp catches for each dive site based on a single trap-night of effort, but also traps generally were set at depths greater than the observed range of maximum abundance determined from our submersible observations (~750 m vs. 550–675 m). This results in no estimate of error for CPUE estimates at each site and no way to determine whether the traps were set within the range of maximum shrimp abundance at the time of trapping. If the traps were not set within this zone, yields at our sites may underrepresent relative shrimp abundance, leading to a lower-than-actual estimate of q. Another potential source of error in our q estimate is the accuracy of our density estimate. Confidence limits on our density estimates are quite broad, allowing for a fair degree of error. At many dive sites this problem is related to the few observations of density taken within the zone of maximum abundance. Additional problems in density estimation associated with the presence of bait in the water during the dives have already been addressed. The question of compatibility between data pairs of density estimates and CPUE values obtained at different points in time stems from possible changes in density or in q over time. Although trap catch rates in the Mariana Archipelago did not vary significantly on a seasonal basis (Polovina et al. 1985), suggesting that q does not vary seasonally, *H. laevigatus* may undergo temporal changes in depth range on either a diurnal or seasonal basis (King 1984, Dailey and Ralston 1986). If such movements do occur (the evidence is not strong) and depth range expands or contracts during these changes, densities observed during midday periods in February and August may differ from those occurring during trapping in March. Finally, although the fit is quite good, our estimate of q is based on only five data pairs covering limited values of CPUE and density.

The potential error in the Ralston and Tagami (1992) q estimate depends on the appropriateness of using their habitat area estimate in normalizing q and the validity of the assumption of constant catchability for all members of the population. These error sources are not necessarily greater than those discussed above, but are much easier to quantify. Even when an accurate estimate of biomass is obtained for a study site, calculation of a normalized q is dependent on the estimated habitat area of the study site. Estimated habitat area is apt to be larger when depth range is estimated from trap catches, as opposed to visual surveys, because of the ability of the traps to draw shrimp outside of their normal depth range. Recalculating the habitat area of the Ralston and Tagami study site using the observed depth range (550–675 m) instead of the reported range (420–640 m) results in a reduction in area to 63% of the original value (748 ha instead of 1187 ha). Normalizing q with this reduced study-site area estimate gives an adjusted q value of 5.999 ha/trap-night (CI 2.6709–9.3271 ha/trap-night. The ratio of this adjusted value to the q obtained in the present study is 20.7 instead of the original 32.7. Ralston and Tagami (1992) discuss the effect on their q value of a large portion of the population not being susceptible to trap capture for the duration of the study period. They supply evidence that their original estimate of catchability may have been four times too high, resulting in a four-fold underestimation of exploitable biomass. Other authors have reported similar overestimates of catchability resulting from depletion studies (Morgan 1974, Morrissy 1975, Miller 1990). A further four-fold reduction of the Ralston and Tagami q value results in a ratio of 5.9 relative to our q value and only 1.8 for the extremes of the 95% CL (the minimum value for the Ralston and Tagami confidence interval compared with our maximum value). Coupling these quantifiable factors with the non-quantifiable factors discussed above could bring the two estimates of catchability into agreement.

Because of the importance of accurate estimates of exploitable biomass to the management process, it would be desirable to conduct a combined technique survey of the *H. laevigatus* resource. This should include direct visual density estimation with a trapping study conducted at the same time and place to obtain a reliable estimate of catchability and thereby exploitable biomass. Until that time, the expanded exploitable biomass estimate (1050 t) for the main Hawaiian Islands as presented by Ralston and Tagami (1992) should be accepted for management purposes as a reasonable, conservative approximation.

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Abstract.– Research and commercial trapping data show variation in recruitment to the fishery for spiny lobster *Panulirus marginatus* at Maro Reef, relative to Necker Island which is 670 km to the southeast. Recruitment to the fishery at Maro Reef is shown to be highly correlated with the difference in sea level 4 years earlier between French Frigate Shoals and Midway Islands. Geosat altimeter data indicate that the relative sea level between French Frigate Shoals and Midway is an indicator of the strength of the Subtropical Counter Current. Mechanisms linking the Subtropical Counter Current with larval advection and survival are discussed. The sea level index provides a forecast of recruitment 4 years later to the fishery at Maro Reef.

Variability in spiny lobster *Panulirus marginatus* recruitment and sea level in the Northwestern Hawaiian Islands*

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Significant correlations between commercial landings or recruitment estimates and one or more environmental indices are commonly reported in the fisheries literature, but few have served as accurate predictors of future population levels (Drinkwater and Myers 1987). However, such correlations can lead to the formulation or support of hypotheses regarding the factors responsible for population changes. For example, an inverse correlation between the survival of Pacific mackerel *Scomber japonicus* to age 1 and the strength of the California Current, and the lack of correlation between survival and plankton biomass, have been offered as evidence that advection, rather than starvation, controlled survival of the planktonic stages of this species (Sinclair et al. 1985).

Correlative studies on lobsters suggest that population size results from changes in survival and advection at the larval stage, but in at least one instance, density-dependent mechanisms after postsettlement may dampen this variation (Pollock 1986). Fluctuations in sea-surface temperature appear to result in changes in larval survival and catches 6 years later for the clawed lobster *Homarus americanus* in Maine (Fogarty 1988). Variation in the strength of the Leeuwin Current, which may be linked to El Niño Southern Oscillation (ENSO) events, is suggested as a cause of variation in the number of larvae returned to the coast and subsequent recruitment to the fishery for the western rock lobster *Panulirus argus* (Pearce and Phillips 1988). Changes in recruitment levels of the California spiny lobster *P. interruptus* to the northern portion of its habitat may be episodic, influenced by large-scale, interannual El Niño events (Pringle 1986). Variation in postlarval recruitment in the South African rock lobster *Jasus lalandii* is thought to arise from changes in the paths and velocities of extensive offshore currents, which eventually return larvae to the coast. However, density-dependent phenomena influ-

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encing juvenile and adult stages may substantially dampen this variation and produce fairly stable recruitment to the fishery (Pollock 1986).

In the Northwestern Hawaiian Islands (NWHI), a substantial drop in catches and catch-per-unit-effort (CPUE) of spiny lobster *P. marginatus* Quoy and Gaimard 1825 was recently documented (Polovina 1991). This study examines whether these declines in catches and CPUE are due to overfishing or to oceanographic factors which impact spiny lobster population dynamics.

NWHI lobster fishery

The NWHI region is an isolated range of islands, islets, banks, and reefs that extend 2775 km northwest from Nihoa Island to Kure Atoll (Fig. 1). In 1977 after research cruises documented a substantial lobster population in the NWHI, a commercial trap fishery was initiated. The fishery targeted two species: the endemic spiny lobster *P. marginatus* and the slipper lobster *Scyllarides squammosus* Mike-Edwards 1837. A fishery management plan implemented in 1983 mandated that vessels submit logbooks recording daily catch and number of traps set (effort); the plan also established a minimum harvest size for spiny lobster and prohibited the harvest of egg-bearing females. Subsequent amendments to this plan added a minimum legal size for slipper lobster and required that traps have escape vents. In 1990, low catches and CPUE prompted a 6-month closure of the fishery (May–November 1991).

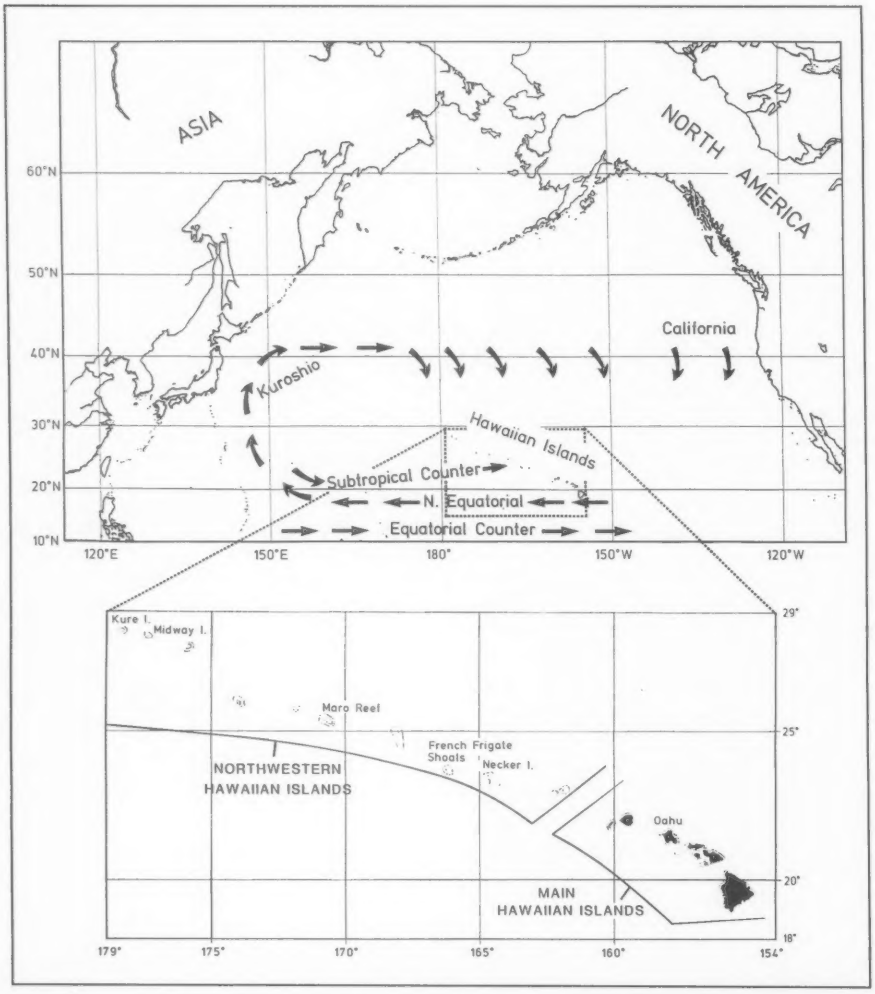

Figure 1
Pacific Ocean and major currents with an inset of the Hawaiian Archipelago, including the Northwestern Hawaiian Is.

Since 1983, the lobster fleet has been composed of 9–14 vessels (20–30 m long), each averaging 3 trips per year. The vessels set about 800 traps per day and remain at sea almost 2 months per trip. Landings in recent years have averaged almost 1 million lobsters, valued at about US$6 million ex-vessel. Because of heavy fishing since 1986, the population has been fished down to the point that 3-year-old recruits comprised most of the fishery catches (Polovina 1991). Since 1988, about 80% of landings have been spiny lobster (Table 1). Two banks—Necker I. at the southeast end of the NWHI, and Maro Reef which is 670 km northwest of Necker I.—account for over 60% of the fishery's catches. There is no recreational lobster fishery in the NWHI.

Table 1

Annual landings of spiny (*Panulirus marginatus*) and slipper (*Scyllarides squammosus*) lobsters, trapping effort, and percentage of spiny lobster in the landings, 1983–90.[1]

Year	Lobster landings (10^3)			Trap hauls (10^3)	CPUE	% spiny lobster
	Spiny	Slipper	Total			
1983[2]	158	18	176	64	2.75	90
1984	677	207	884	371	2.38	78
1985	1022	900	1922	1041	1.83	53
1986	843	851	1694	1293	1.31	50
1987	393	352	745	806	0.92	53
1988	888	174	1062	840	1.26	84
1989	944	222	1166	1069	1.09	81
1990	591	187	778	1182	0.66	76

[1] Data were provided to the NMFS Honolulu Lab., as required by the Crustacean Fishery Management Plan of the W. Pac. Reg. Fish. Manage. Counc., Honolulu.
[2] April–December 1983.

Spiny lobster spawn over a broad spring, summer, and fall period. After hatching, the eggs are planktonic; the planktonic period for the larvae is estimated at 12 months based on spawning season and larval tow data (NMFS Honolulu Lab., unpubl. data). Further, the larval tow data suggest that mid- to late-stage spiny lobster larvae are close to the surface at night and move down to ~100 m during the day (Polovina, pers. observ.). Based on growth curves estimated from both tagging (MacDonald 1984) and length-based methods (Polovina and Moffitt 1989), spiny lobster reach the minimum legal size (which is slightly larger than the size at onset of sexual maturity) approximately 3 years after they settle onto benthic habitat. After settlement, the lobster probably do not move between banks since interbank depths exceed 1000 m.

Regional oceanography

The Hawaiian Archipelago lies within the subtropical gyre formed by the Kuroshio Current to the west and the north, the California Current to the east, and the North Equatorial Current to the south (Fig. 1). The speed of the gyre in the vicinity of the archipelago is slow (<5 cm/s; Roden 1991). An eastward-flowing current within the subtropical gyre, named the Subtropical Counter Current (SCC), was predicted by Yoshida and Kidokoro (1967) and subsequently confirmed by Robinson (1969) and Uda and Hasunuma (1969) (Fig. 1). More recent work has shown that, in at least the western portion, the interior of the subtropical gyre is composed of a quasi-stationary banded structure of easterly- and westerly-flowing currents (White and Hasunuma 1982). The SCC consists of two bands of eastward flow at 23° and 28°N, with mean annual speeds of 8 and 6 cm/s, respectively (White and Hasunuma 1982).

In addition to these large-scale features, the mesoscale oceanography around the Hawaiian Archipelago is a complex system of fronts and eddies resulting from both interactions between alternating east and west currents and interactions between current and the topography of the archipelago.

Data and analysis

Research data

Standardized trapping surveys, using the same traps set at the same sites, were conducted at Necker I. and Maro Reef during June and July of 1986–88 and 1990. The size-frequency data were converted to age-frequency data with a von Bertalanffy growth curve (MacDonald 1984). The age-frequency distribution was standardized for the number of traps deployed to estimate the relative age-frequency distribution of the population.

Fishery data

Although detailed catch and effort data were not available until after the logbook regulations were established in 1988, catch and effort were generally light and were concentrated around Necker I. from the inception of the fishery until 1984 (Fig. 2). The combined CPUE for slipper and spiny lobsters in 1983–90 generally declined from 2.8 to ~0.7 lobster per trap-

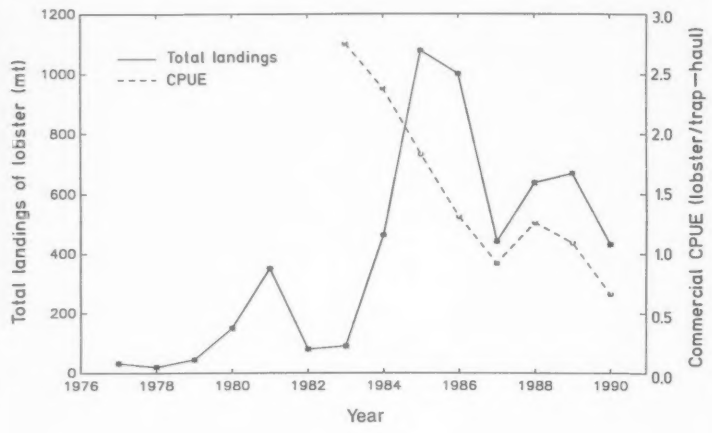

Figure 2

Total slipper (*Scyllarides squammosus*) and spiny (*Panulirus marginatus*) lobster landings and CPUE from the Northwestern Hawaiian Is., 1977–90.

haul (Fig. 2), based on catch and effort data reported in the logbooks. Catch data in the logbooks are checked against landings by enforcement agents, so misreporting is not a problem. Common assessment approaches, such as length-based cohort analysis, are not applicable to this fishery, given the relatively short time-series of catch and effort data, the difficulty in routinely ageing lobsters, and the lack of information on the size-frequency from the landings and the nature of a stock-recruitment relationship. While a dynamic surplus production model has been applied to the data, an implicit assumption about the form of the stock recruitment relationship is required (Polovina 1991).

A more general approach is to begin with a model which expresses N_t as the number of exploitable lobsters at time t as a function of N_{t-1}, Z as the total instantaneous mortality from time $t-1$ to t, and r as the number which recruit and survive from $t-1$ to t as

$$N_t = r + N_{t-1}\, e^{-z}.$$

Using the relationship that the product of catchability (q) and $N_{(t)}$ is $CPUE_{(t)}$, this model becomes

$$CPUE_t = q*r + CPUE_{t-1}\, e^{-M-qf},$$

where M and f are annual instantaneous natural mortality and fishing effort, respectively, during the period $t-1$ to t. This CPUE model, a simple version of a size-structured model developed by Schnute et al. (1989), was used to estimate population parameters and to evaluate the extent that fishing effort explains the observed variation in CPUE. This model assumes constant catchability and recruitment; hence, the differences between predicted and observed CPUE are interpreted as variation in recruitment, catchability, or both.

The commercial data do not indicate whether effort was directed at slipper or spiny lobster. However, the catches can be grouped into two periods based on the proportion of spiny to slipper lobsters. In period 1 (1983–84 and 1988–90), ~80% of the landings were spiny lobster; in period 2 (1985–87), ~56% of the landings were spiny lobster (Table 1). The change in proportion of spiny lobster catches is likely due to changes in targeting and abundance. The CPUE model is modified so that a catchability coefficient can be estimated for each period. Our modified CPUE model regresses the CPUE of spiny lobster above the minimum size in month t ($CPUE_t$) on the CPUE of the same month in the previous year:

$$CPUE_t = R*Q_t\, e^{-\frac{(M+Q_t f_t)}{2}} + (CPUE_{t-12})\,(e^{-M-Q_t f_t})\left(\frac{Q_t}{Q_{t-12}}\right)$$

with

$$Q_t = q_1 I_{1,t} + q_2 I_{2,t}$$

where q_1 is the catchability of spiny lobster during period 1, q_2 is the catchability during period 2, M is the annual instantaneous natural mortality, R is the annual recruitment, f is the cumulative fishing effort during the period $(t-12, t-1)$, and $I_{i,t}$ $(i=1,2)$ is the indicator or set function which takes the value 1 if t is within period i or otherwise takes the value 0. Estimates of R, q_1, q_2, and M were obtained by minimizing the sum of squares of the difference between the square root of the observed and predicted CPUE with a simplex algorithm.

Sea level data

To examine the relationship between lobster recruitment variation at Maro Reef and physical factors such

as variation in the SCC, we focused on the analysis of sea level data from the NWHI. Our choice of sea level was primarily a practical one. In comparison to current or upper-layer temperature records, the sea level records are of long duration, and the data are measured continuously and are available in nearly real-time. An additional advantage is that sea-surface height data from the Geosat satellite altimeter are available to provide a spatial description that complements the temporal description available from the sea level stations.

Data on the difference in sea level between the gauges at French Frigate Shoals (FFS) and at Midway Is. have been available since 1976 (Figs. 1,3). This sea level difference (denoted as FFS–Midway sea level) serves as an index of the geostrophic current anomalies across the NWHI in the region of Maro Reef. For example, an increase in the sea level height at FFS relative to Midway Is., measured from tide gauges, indicates the strengthening of a current that is across the gradient between the two locations and is flowing from the southwest to the northeast.

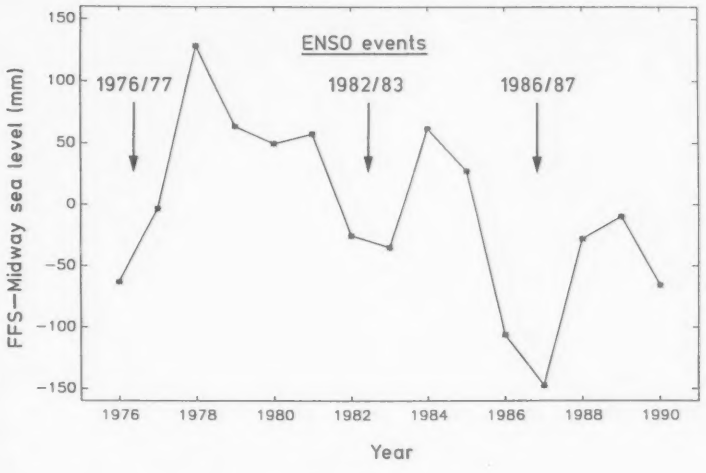

Figure 3
Annual French Frigate Shoals (FFS)–Midway sea level differences from tide gauges, 1976–90 (ENSO = El Niño Southern Oscillation).

To interpret these flow anomalies as a manifestation of the variations in SCC strength, the spatial structure of the sea-surface height variation was examined by mapping the variability observed by the Geosat altimeter during November 1986–November 1988. These 2 years were selected because more accurate orbit estimates were available during this time-period and would result in more accurate sea-surface height fields. The Geosat geophysical data records were obtained from NOAA (Cheney et al. 1987) and were processed with software developed at the University of Hawaii.

Averages of the Geosat data over November 1986–November 1987 were subtracted from the averages over November 1987–November 1988. Before using the Geosat data, we checked that the resulting sea level differences from the altimeter were consistent with the corresponding sea level differences from tide gauges at FFS and Midway (not shown). Choosing these time-periods also allowed us to contrast conditions during the ENSO period of 1986–87, when the FFS–Midway sea level was low (~520 mm), with conditions during the normal period of 1987–88, when the FFS–Midway sea level was higher (~600 mm).

Puerulus settlement

During the last planktonic stage (i.e., postlarval or puerulus stage), spiny lobster acquire the benthic morphological features of adults and become active swimmers seeking benthic habitat. MacDonald (1986) studied puerulus settlement in the Hawaiian Archipelago with traps known as Witham Collectors at Kure Atoll (north of Midway Is.) in 1979–83 and at FFS in 1981–85. He computed mean catch per collector over 12-month periods (June–May) at Kure Atoll and FFS. These data will be compared with the FFS–Midway sea level data.

Results

The fit of the model to the commercial CPUE data and the resulting residuals indicate the model fits the trend in CPUE, but considerable unexplained variation exists in CPUE within and between years (Fig. 4). For example, given the fishing effort, CPUE was greater than expected in 1988 but declined more than expected in 1990. Since the model assumes both constant recruitment and constant catchability, the residuals may reflect variation in these factors. From the fit of the model, $R = 1.2 \times 10^6$ adult lobsters/yr, $M = 0.71$/yr, $q_1 = 1.2 \times 10^{-6}$, and $q_2 = 0.6 \times 10^{-6}$. Thus 1.2 million lobsters recruit to the fishery annually; with an M of 0.71/yr, only 50% of the 3-year-olds survive 1 year (in

the absence of fishing). Further, a CPUE of 1.2 spiny lobster/trap-haul means the exploitable population is 1 million spiny lobster. An independent estimate of M from tagging at FFS is 0.5/yr (MacDonald 1984).

Commercial trapping effort since 1985 has averaged about 1 million trap-hauls (Table 1); using the q_1 estimate as catchability, annual fishing mortality (F) is estimated as 1.2/yr or 1.7 × M. With these figures and the estimates of growth and age at onset of sexual maturity, the Beverton-Holt yield equation estimates the spawning-stock biomass per recruit, when effort is 1 million trap-hauls, is 40% of what it would be in the absence of fishing (Polovina 1991). Thus, the ratio of F to M and the relative spawning-stock biomass calculations suggest that the spawning biomass in 1985–86 was not fished down to a level that would cause the poor recruitment to the fishery 4 years later (1989–90).

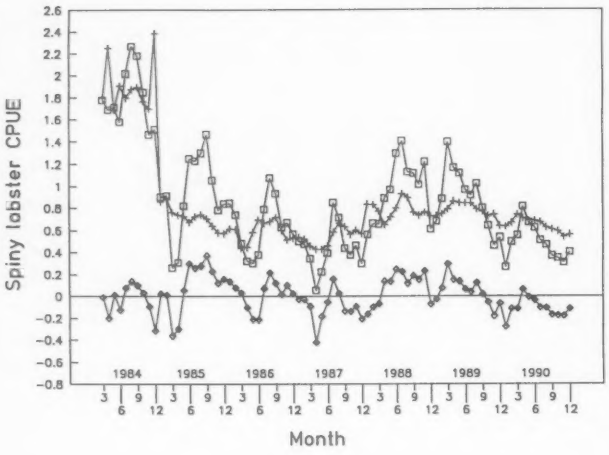

Figure 4

Fit of the CPUE model (+) to monthly CPUE (□) for spiny lobster *Panulirus marginatus* in the Northwestern Hawaiian Is., and residuals from the fit (◆).

Much of the variation in residuals from the CPUE model is due to variation in recruitment at Maro Reef. For example, for the entire NWHI in 1990, trapping effort increased 11% from the previous year while the catch declined 33%, resulting in a 39% decline in CPUE. However, the decline in CPUE was most striking at Maro Reef, where CPUE declined 42% even though effort decreased by 37%. At Necker I., CPUE also declined (40%) but effort increased 35%.

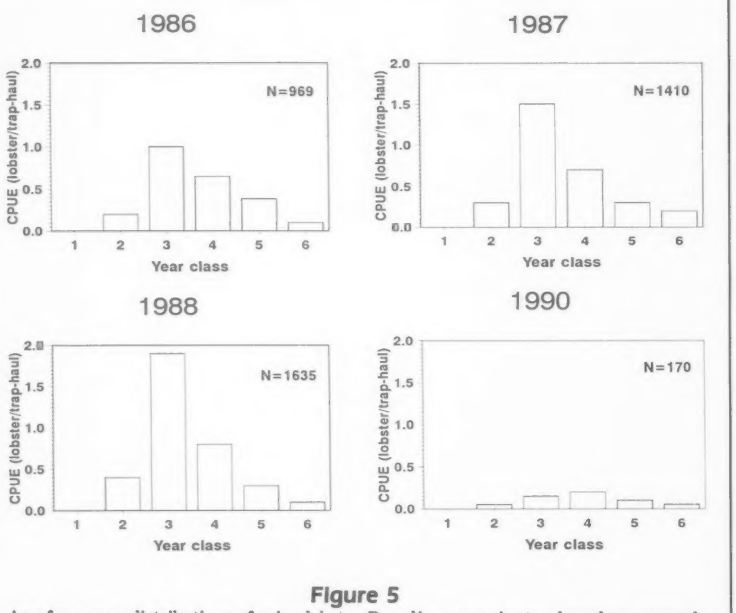

Figure 5

Age-frequency distributions of spiny lobster *Panulirus marginatus*, based on research sampling in 1986–88 and 1990 at Maro Reef (N = no. of spiny lobster in the sample).

The estimated age-frequency distributions based on research cruises at Maro Reef show a strong 3-year-old class in 1988 and a striking absence of all age-classes in 1990 (Fig. 5). This is consistent with the hypothesis that recruitment of the 3-year-olds to the fishery was weak in 1990 and subsequent fishing reduced all older age-classes. Necker I. had many more 2-year-olds in the samples since some trapping sites include nursery habitat; but between years, the abundance of 2-year-olds was relatively constant, whereas older lobsters declined in 1990, likely because of the increase in fishing effort (Fig. 6).

The NWHI lobster fleet is very mobile and shifts its trapping locations according to abundance of lobsters. By 1985, both Maro

Reef and Necker I. had gone through a period of fishing down the pre-exploitation population; the relative change in catches between the two banks may reflect changes in their relative recruitment. Since both banks are not always fished each month, we pooled the catches by quarter. A 3-quarter moving average of the ratio of quarterly catches at Maro Reef to the combined quarterly catches at Necker I. and Maro Reef shows considerable variation (Fig. 7). For example, catches from Maro in 1985 and 1988 represented almost 80% of the catches from the two banks, but in 1990 they represented less than 20%. A 3-quarter moving average of the residuals from the CPUE model shows the same trend as the ratio of catches from Maro Reef relative to Necker I. and Maro Reef combined (Fig. 7). This suggests that the variation in recruitment, catchability, or both at Maro Reef is responsible for most of the variation not explained by fishing effort observed for the entire NWHI.

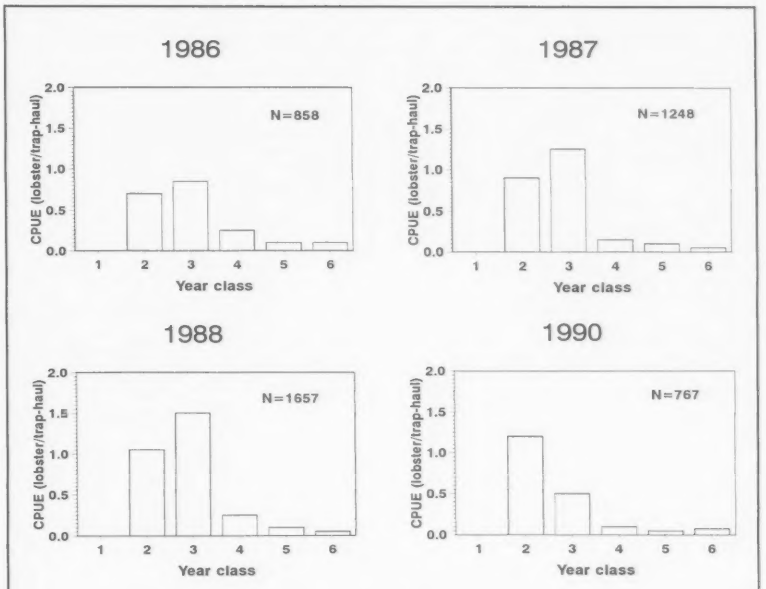

Figure 6
Age-frequency distributions of spiny lobster *Panulirus marginatus*, based on research sampling in 1986–88 and 1990 at Necker I. (N = no. of spiny lobster in the sample).

Variation between sea level and the SCC

Differences in sea level over the Pacific, between a year when the FFS–Midway sea level was high and a year when it was low, appear as a ridge of positive values, extending from southwest to northeast, that parallels a trough of negative values to the northwest (Fig. 8). Midway lies in the trough, Honolulu is on the ridge, and FFS lies on the gradient, which corresponds to the region of the most energetic geostrophic flow anomalies. This ridge and trough indicate that the change in the FFS–Midway sea level from low to high reflects the increase in a ridge extending across the western Pacific. The increase in the ridge and trough pattern represents an increase in the current flow along the gradient of this ridge. The path of this gradient or flow across the Pacific is consistent with the general path of the SCC. Thus FFS–Midway sea level measures a large-scale oceanographic feature which is represented by the height of the sea level ridge stretching across the Pacific. The height and location of this sea level ridge

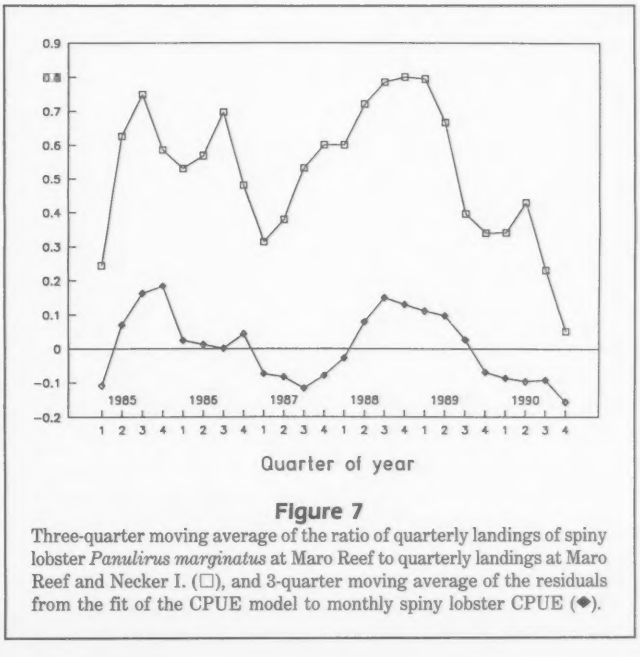

Figure 7
Three-quarter moving average of the ratio of quarterly landings of spiny lobster *Panulirus marginatus* at Maro Reef to quarterly landings at Maro Reef and Necker I. (□), and 3-quarter moving average of the residuals from the fit of the CPUE model to monthly spiny lobster CPUE (◆).

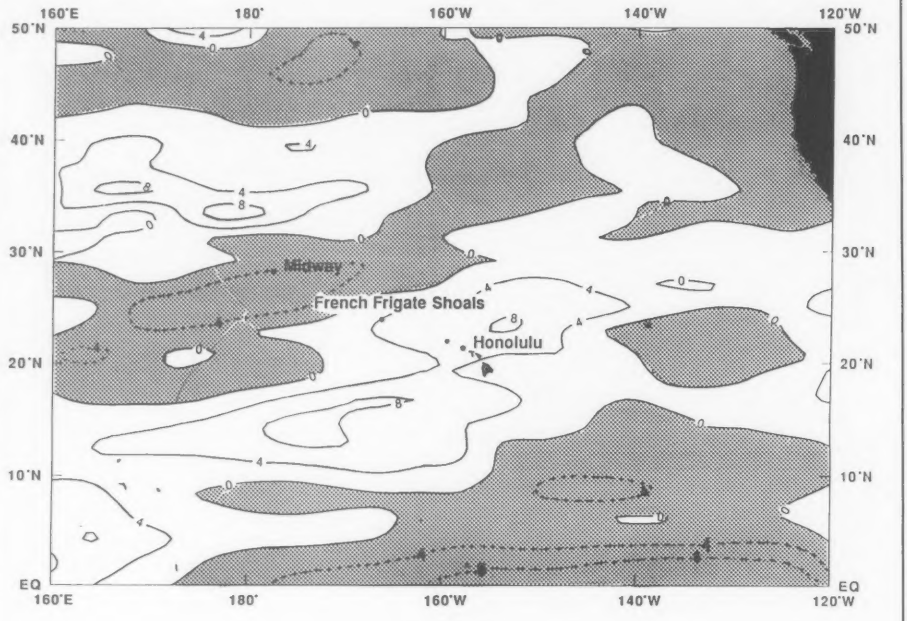

Figure 8

Differences between mean sea level during a non-ENSO (El Niño Southern Oscillation) period (Nov. 1987–Sept. 1988) and an ENSO period (Nov. 1986–Sept. 1987) from Geosat data. Negative values denoted by shaded areas.

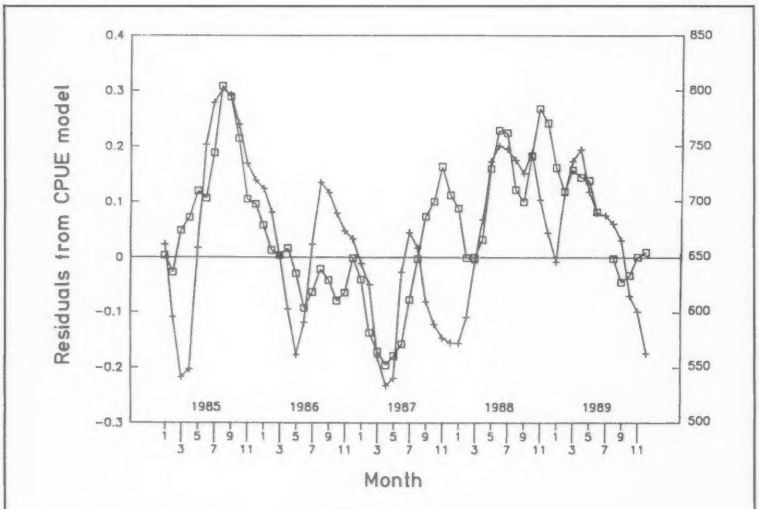

Figure 9

Overlay of 3-month moving average of French Frigate Shoals (FFS)–Midway sea level advanced by 4 years (□) with a 3-month moving average of residuals from the fit of the CPUE model (+).

correspond to the SCC strength and position, respectively.

Relationship between sea level and lobster abundance

Lagged cross-correlations between FFS–Midway sea level and the variables (i.e., the ratio of catches at Maro Reef to the combined catches at Maro Reef and Necker I., and the residuals from the CPUE model) have their strongest correlations (r 0.82 and 0.68, respectively) with sea level lagged by exactly 4 years. When sea level is lagged by 4 years and overlayed with these time-series, there is good agreement (Figs. 9,10). Based on research samples pooled over 1986–88, the mean estimated age of lobsters caught by the fishery is 3.8 years (after settlement).

Based on the comparison of FFS–Midway sea level with the available puerulus settlement data from MacDonald (1986) in the same year, the FFS–Midway sea level correlates positively with mean puerulus catches at Kure Atoll (r 0.78, P 0.11) and shows no significant correlation with mean puerulus catches at FFS (r −0.37, $P>0.25$) (Fig. 11).

Discussion

The research and commercial catch and effort data presented here show that the recruitment of 3-year-old spiny lobster to the fishery has varied considerably at Maro Reef but has remained stable at Necker I., 670 km to the southeast. Fishing effort is not considered sufficiently heavy to explain a decline in recruitment, especially a decline at one bank and not the other. The relationship between recruitment to the fishery at Maro Reef and the FFS–Midway sea level advanced by 4 years suggests that environmental factors impacting the larval stage are responsible for the recruitment variation. The Geosat data suggest that the FFS–Midway sea level measures the SCC. Hence the SCC strength or location dictates recruitment strength to the fishery 4 years later. Consistent with this hypothesis is the mean age of lobsters in the commercial catches as well as the correlation between puerulus settlement at Kure Atoll and FFS–Midway sea level. The lack of correlation between puerulus settlement at FFS and sea level is consistent with the observation that recruitment at the lower end of the NWHI is not linked to the same pattern of variation as Maro Reef. Annual variation in both SCC strength and position has been observed in the western Pacific (White and Hasunuma 1982). In summary, the temporal pattern of spiny lobster recruitment differs between Necker I. and Maro Reef. At Maro Reef, large-scale oceanographic features appear to control the abundance of late-stage larvae, which in turn results in interannual variation in recruitment to the fishery.

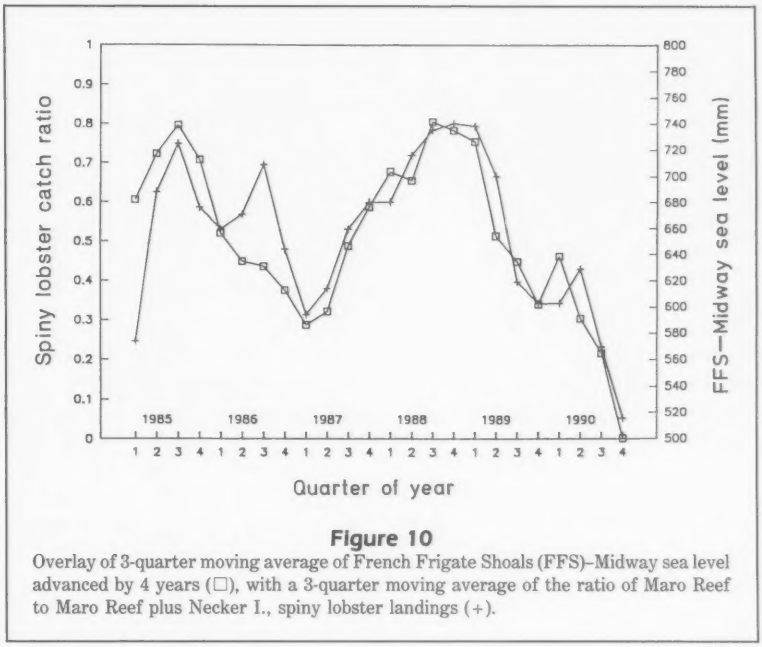

Figure 10
Overlay of 3-quarter moving average of French Frigate Shoals (FFS)–Midway sea level advanced by 4 years (□), with a 3-quarter moving average of the ratio of Maro Reef to Maro Reef plus Necker I., spiny lobster landings (+).

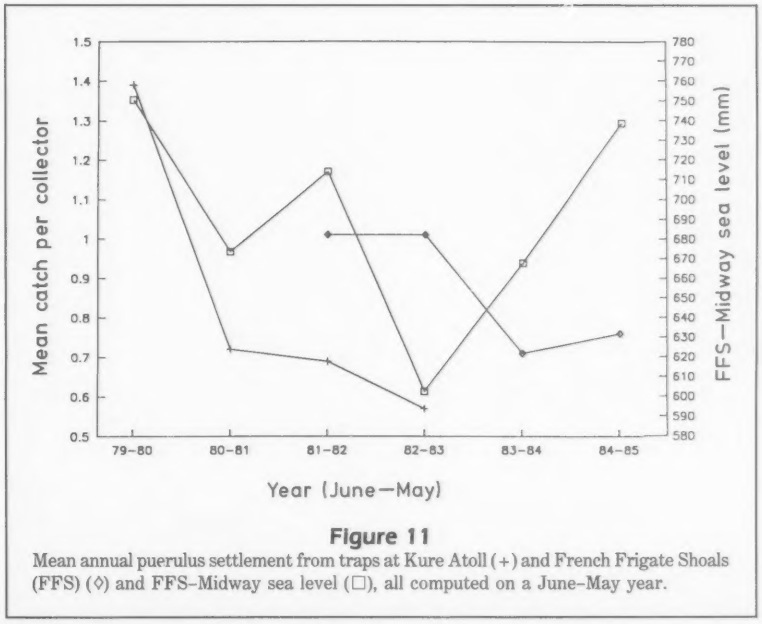

Figure 11
Mean annual puerulus settlement from traps at Kure Atoll (+) and French Frigate Shoals (FFS) (◇) and FFS–Midway sea level (□), all computed on a June–May year.

The underlying mechanism linking the correlation between the SCC and subsequent recruitment at Maro Reef is not known. It is possible that the SCC returns larvae, which have been advected west of the archipelago, back to Maro Reef. The SCC has been hypothesized to transport *Acropora* coral from Johnston Atoll (lat. 16°45′N., long. 169°31′W) to FFS (Grigg 1982). In addition, larvae of a spiny lobster species not recorded as an adult in Hawaii have been transported from the Marshall Is. to the Hawaiian Archipelago (Phillips and McWilliam 1989).

However, it may be that the SCC impacts not advection but larval survival. Laboratory studies have shown that spiny lobster larvae suffer a high level of mortality when water temperatures drop below 20°C (T. Kazama, NMFS Honolulu Lab., pers. commun., Sept. 1991). In the years we estimated that the SCC was weak, water temperatures <20°C in the winter have been observed at Maro Reef but not Necker I. If little larval mixing occurs between Maro Reef and Necker I., larval mortality at Maro Reef resulting from low winter temperatures could account for the observed recruitment variation.

A third hypothesis is that when the SCC has a particular speed and location, it produces fronts which retain larvae near Maro Reef. When the SCC is weak or shifts, these fronts are not formed near Maro Reef. Preliminary evidence from the drifter buoys and larval sampling in our study suggests fronts north of Maro Reef and south of Necker I. may be important for lobster larvae (Polovina, pers. observ.)

One potential management application of the lagged relationship between FFS–Midway sea level and recruitment is that it provides up to a 4-year forecast of recruitment to the fishery at Maro Reef. A 3-quarter moving average of the FFS–Midway sea level shifted forward by 4 years forecasts poor recruitment in 1991, followed by an improvement beginning in late 1992 (Fig. 12). During January–May 1991 before the fishery was closed for 6 months, recruitment at Maro Reef clearly had not recovered, as only 1052 spiny lobster were harvested from Maro Reef while 34,746 spiny lobster were harvested from Necker I. Recall that the relative catches between banks provide an index of relative abundance, since the fleet moves to maximize the CPUE. The FFS–Midway sea level data forecast that catches at Maro Reef will improve beginning in late 1992 (Fig. 12). Data from larval tows are consistent with this forecast. Standardized larval tows, taken in June and November 1989 over a grid of stations from the 200 m isobath out to 56 km around both Necker I. and Maro Reef, caught 3802 and 3342 late-stage phyllosomes, respectively (J. Polovina, unpubl. data). A t-test, based on a lognormal distribution, finds no significant difference in the mean abundance of larvae between Maro Reef and Necker I. If we assume that larval abundance was high around Necker I. in 1989, then good larval recruitment apparently has returned to Maro Reef. This is consistent with the observed higher sea-level values in 1989 (shown as 1993 values in Fig. 12, since the sea level has been advanced by 4 years) and suggests that catches will be high at Maro Reef in 1993.

The FFS–Midway sea level time-series from 1976 to 1990 (Fig. 3) shows that ENSO events may result in poor recruitment to the fishery 4 years later, but the series also shows a long-term decline. Reasons for the low FFS–Midway sea level during ENSO events are not known, but may be related to a decrease in surface water supplied to the SCC in the western Pacific. Such a change could be associated with the circulation disruptions observed in the tropical Pacific during ENSO events (Meyers and Donguy 1984). The long-term decline in sea level from 1976 to 1990 suggests there is a low-frequency component in the variation in SCC strength and, hence, lobster recruitment. Thus, it may be some time before recruitment to the fishery is at the early 1980s' level.

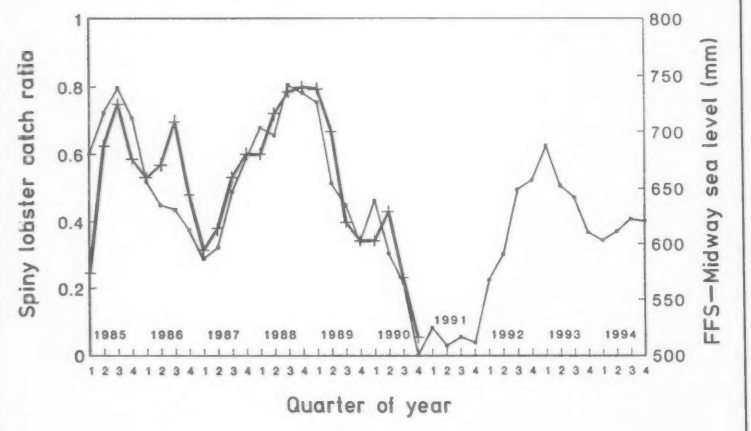

Figure 12

Three-quarter moving average of the ratio of quarterly landings of spiny lobster *Panulirus marginatus* at Maro Reef to quarterly landings at Maro Reef and Necker I. (bold line) overlayed with the 3-quarter moving average of French Frigate Shoals (FFS)–Midway sea level deviation advanced by 4 years (thin line).

Acknowledgments

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An assessment of the exploitable biomass of *Heterocarpus laevigatus* in the main Hawaiian Islands. Part 1: Trapping surveys, depletion experiment, and length structure

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Abstract. – A deepwater trapping survey for *Heterocarpus laevigatus* was conducted around the main islands of the Hawaiian Archipelago to estimate exploitable biomass and potential yield. Stratified sampling by depth zone and island was conducted over a 3-year period to evaluate shrimp catch rates. Catchability of the traps was estimated from a 12-day intensive fishing experiment performed at a small, isolated site in the Kaulakahi Channel; habitat areas were determined by digitizing nautical charts.

Results from a Leslie analysis of the depletion experiment showed that *H. laevigatus* is very susceptible to capture by traps (i.e., catchability $\hat{q}$ = 9.48 ha/trap-night). There was no evidence of a change in size structure through the course of the experiment.

Shrimp catch rates varied greatly by island and depth of capture. Exploitable biomass was greatest in the 460–640 m depth range; negligible amounts of shrimp occurred shallower than 350 m and deeper than 830 m. Catch rates were highest at Niihau and lowest at Oahu. The total exploitable biomass of shrimp in the main Hawaiian Is. was estimated to be 271 MT, a figure substantially less than previously believed.

Analysis of multiple size-frequency distributions for each sex showed no evidence of modal size progression. Assuming equilibrium conditions, application of the Wetherall et al. (1987) method to these data resulted in estimates of M/K = 1.01 for female shrimp and 0.74 for males. From these results and estimates of L_∞ we calculate that $F_{0.1}/M = 0.75$ for females and 0.86 for males.

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The caridean shrimp, *Heterocarpus laevigatus* Bate 1888, is an abundant deepwater inhabitant of the Hawaiian Is., where it has been fished sporadically since 1970 (Anon. 1979). Two early research surveys (Clarke 1972, Struhsaker and Aasted 1974) showed that large catches of this species, and its smaller congener *H. ensifer*, could readily be taken in baited traps in water depths of 365–825 m (200–450 fm).* Based on catch rates from around the island of Oahu, the deepwater shrimp resource seemed sufficiently abundant to support a commercial fishery (2.6 kg/trap-night for *H. laevigatus* and 6.6 kg/trap-night for *H. ensifer*; Struhsaker and Aasted 1974).

To date, however, attempts to harvest the resource have met with limited success, even though 75 MT of *H. laevigatus* were landed by one vessel during a 14-month period (Tagami and Barrows 1988). At its peak in 1983–84, a short-lived fishery developed, involving as many as 7 medium-sized (23–40 m) boats. At that time over 190 MT of *H. laevigatus* were landed, with an ex-vessel value of $1.5 million ($7.85/kg; Hawaii Dep. Land & Nat. Resour., Div. Aquat. Resour.). The fishery soon failed, however, primarily due to problems with gear loss, product processing, and localized stock depletions. Even so, the product was well received by the public, and rejuvenating the shrimp fishery remains a fishery development goal of the State of Hawaii (Anon. 1984).

With this interest in developing the Hawaiian fishery, major gaps in our knowledge of local *H. laevigatus* shrimp stocks have become apparent (see Gooding 1984, Dailey and Ralston 1986), although elsewhere in the Pacific more extensive data are available (e.g., Wilder 1977, King 1984 and 1986, Ralston 1986, Moffitt and Polovina 1987). Particularly lacking are estimates of the absolute abundance of the *H. laevigatus* stock in Hawaii and its ability to withstand sustained fishing pressure.

The primary objective of the work presented here was to estimate the exploitable biomass of *H. laevigatus* in the main Hawaiian Is. A secondary objective was to estimate growth and mortality rates through analysis of length-frequency data. Together

*Depths are given in meters with fathom equivalents (1.0 fm = 1.83 m), although contouring and stratification were based on nautical charts in fathoms.

these findings could form a basis for estimating the potential yield of the shrimp resource.

To determine the exploitable biomass of shrimp at spatially discrete locations in Hawaii, the formula (Ricker 1975) was used:

$$\text{CPUE} = q\left[\frac{B}{A}\right]$$

where CPUE is the catch-per-unit-effort, q is the catchability coefficient of the fishing gear, B is exploitable biomass, and A is the area occupied by the population. This relationship is based on the explicit assumption that catch rate is strictly proportional to shrimp density (B/A), and that q is the proportionality constant equating these quantities. By rearrangement we have,

$$B = \frac{\text{CPUE} \cdot A}{q}.$$

Thus, to estimate the exploitable shrimp biomass at a locality we need (1) an unbiased estimate of catch rate, (2) a measure of the habitat area over which the catch rate prevails, and (3) knowledge of the sampling gear's efficiency (i.e., an estimate of q).

To accomplish these three objectives, the study was divided into two phases. First, a depletion experiment was conducted to estimate the catchability coefficient (q). This was followed by a depth-stratified sampling program for *H. laevigatus* around each of the main islands of the Hawaiian archipelago (i.e., Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, and Niihau).

Methods

Shrimp trapping was conducted during a series of nine cruises of the NOAA ship *Townsend Cromwell* (Table 1). During each cruise, standard fishing gear was utilized to gather CPUE statistics at specific geographical locations. The gear employed was a top-loading pyramidal shrimp trap, identical in construction to those used commercially in Hawaii from 1983 to 1984. Each trap was made of welded steel reinforcement bars, had a 1.83 m^2 base, an overall volume of 1.84 m^3, and was covered by 1.27 × 2.54 cm mesh hardware cloth. A full description and illustration of the gear is given in Tagami and Barrows (1988).

Typically, 6–10 solitary traps were set daily and allowed to soak overnight. Traps were generally deployed in the afternoon and hauled the following morning, being in the water for a period of 16–20 hours. All traps were baited with approximately 3 kg of chopped mackerel *Scomber japonicus*. After hauling to the surface, each trap was emptied and the contents were sorted to species, counted, and weighed to the nearest 0.01 kg. Random subsamples of ~200 *H. laevigatus* were routinely collected, from which carapace length (CL) was measured to the nearest 0.1 mm using dial calipers. For all measured shrimp, sex was determined by examining the endopodite of the first pleopod (spatulate in males, pinnate in females; see King and Moffitt 1984). In addition, the ovigerous condition of females was recorded.

Table 1
Summary of shrimp-trapping cruise dates and locations.

Date	Location	No. of traps hauled
April 1985	Molokai	3
	Lanai	1
May 1986	Kaulakahi Channel	105
July 1986	Kaulakahi Channel	10
Sept. 1986	Kaulakahi Channel	10
Nov. 1986	Kaulakahi Channel	12
Sept./Oct. 1987	Niihau	68
	Kauai	128
	Kaulakahi Channel	11
Feb./March 1988	Kaulakahi Channel	10
	Oahu	8
	Hawaii	31
Oct. 1988	Kaulakahi Channel	17
	Molokai	20
	Lanai	18
	Maui	38
	Kahoolawe	8
March 1989	Oahu	67
	Molokai	32

Depletion experiment

To estimate q, an intensive fishing experiment was conducted (see also Ralston 1986). Depletion experiments, including the Leslie method used here (Ricker 1975), have three restrictive assumptions. First, all individuals in the exploitable portion of the population are equally likely to be captured with the fishing gear. Second, the fished population is closed, or else additions exactly balance removals other than those due to fishing. Third, fishing removals account for all changes in stock biomass, such that natural mortality, growth, and recruitment have negligible effects during the period of fishing. Thus, the best site for a depletion experiment is a naturally isolated, small area so that removals can be carried out over as short a time-interval as possible.

A small rise midway in the Kaulakahi Channel (21° 54.5′N, 159°56.5′W) separating Kauai and Niihau was

chosen for the work. This nearly circular rise (Fig. 1) with a crest at 421m (230fm), has an area of 1187ha (horizontal planar area <640m or 350fm) and is isolated from the Islands of Kauai and Niihau by depths >730m (400fm; Fig. 2). The site lies in the required depth range for *H. laevigatus* and has relatively high densities of the target species.

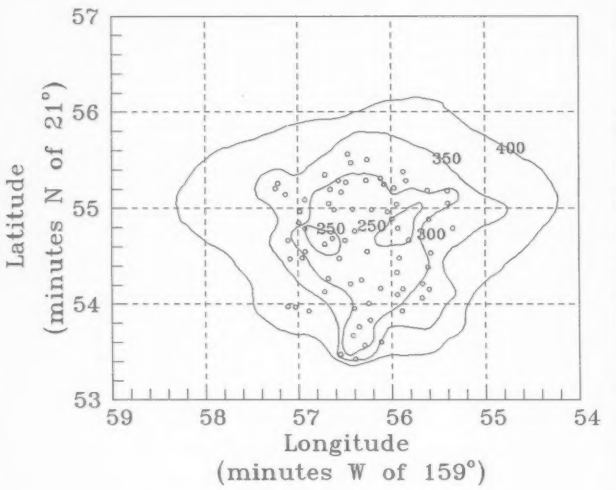

Figure 1
Contour map of the Kaulakahi Channel study site. Depths are in fathoms, and circles represent trap-set locations.

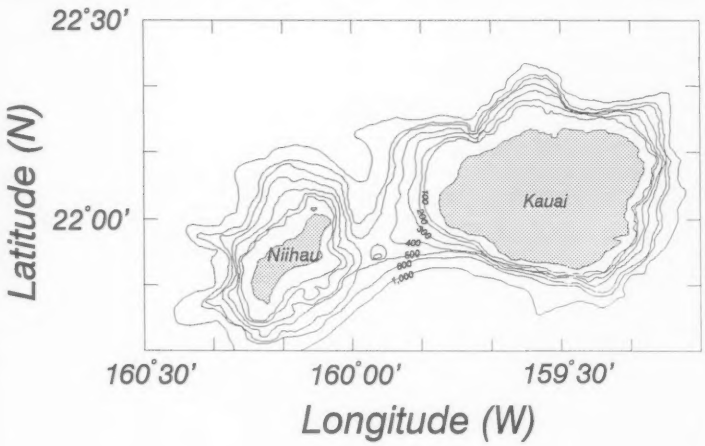

Figure 2
Contour map of the Kauai-Niihau area depicting the 100, 200, 300, 400, 500, 600, and 1000fm isobaths. Note the depletion study site, i.e., the small rise located mid-channel.

The intensive fishing experiment was conducted 13–24 May 1986. During each of the 12 days of the experiment, 6–14 pyramidal shrimp traps were set between depths of 421 and 695m (230 and 380fm). Following the Leslie method (Ricker 1975, Seber 1982), catchability was estimated directly from the slope of the linear regression of CPUE on corrected cumulative catch. That is,

$$\begin{aligned} CPUE_i &= q \cdot B_i \\ &= q(B_0 - K_i) \\ &= qB_0 - qK_i, \end{aligned}$$

where $CPUE_i$ is the catch-per-unit-effort on day i (kg/trap-night), q is the catchability coefficient/trap-night of the pyramid traps, B_i is the average biomass (kg) present on day i, B_0 is the biomass (kg) of shrimp present at the start of the experiment, and K_i is the corrected cumulative removals for day i, defined as

$$K_i = \frac{1}{2} C_i + \sum_{n=1}^{i-1} C_n,$$

where $C_n (n=1,2,\ldots,i)$ is the catch (kg) taken on each day of the experiment. Note that the estimate of catchability ($\hat{q}$) pertains strictly to the interaction between the traps we used and the stock resident in the study area, which is normalized to unit area after multiplying by 1187ha (i.e., the area of the study site).

Determination of habitat areas

The distribution of *H. laevigatus* is strongly dependent on bottom depth. Little or no shrimp occur in waters outside the 366–915m (200–500fm) range (Struhsaker and Aasted 1974, Gooding 1984, Dailey and Ralston 1986). In the main portion of the Hawaiian Archipelago (Hawaii, Maui, Lanai, Kahoolawe, Molokai, Oahu, Kauai, and Niihau) a number of islands share a common 915m (500fm) depth contour (e.g, Kauai and Niihau; Fig. 2). Even so, in our study each island was treated as a separate stock for

purposes of geographically stratifying the analysis. An exception was made for the islands of Maui, Lanai, Kahoolawe, and Molokai (MLKM), which share, in addition to the 915 m (500 fm) contour, a common 366 m (200 fm) isobath. These four islands were, therefore, treated as a single geographic locality.

Estimates of the amount of suitable shrimp habitat, in hectares (1 ha = 0.01 km^2), were obtained by determining the horizontal planar area lying between charted depth contours. A large digitizing tablet was used to calculate all area estimates directly from nautical charts (NOAA charts 19016, 19019, and 19022, and Defense Mapping Agency bottom contour charts). These charts included 915 m (500 fm) isobaths, but we manually contoured all of the 366 m (200 fm) isobaths using the sounding data provided on each chart. In addition, good detailed bathymetry was available for the islands of Kauai and Niihau, and at these sites the 458 m (250 fm), 549 m (300 fm), 640 m (350 fm), 732 m (400 fm), and 824 m (450 fm) isobaths were contoured and digitized as well.

Each contour was digitized three times by each author, providing a minimum estimate of measurement error in our calculation of habitat areas. These errors were typically small (median CV 0.5%, range 0.1–1.9%). A potentially more serious type of error concerns discrepancies between the actual locations of contours and their representations on charts. However, we had no information concerning the magnitude of this type of error and, given that measurement errors were negligible, we assumed that our estimates of habitat area were accurate and precise.

These data were then used to calculate habitat areas for each 92 m (50 fm) depth interval between 366 and 915 m (200–500 fm). First, the relative distribution of habitat was calculated from the Kauai and Niihau data. To estimate depth-specific habitat areas for the three remaining sites (Oahu, MLKM, and Hawaii), the combined relative proportions of habitat for each depth interval obtained at Kauai–Niihau were applied to the estimates of total habitat area between 366 and 915 m (200–500 fm). In support of this procedure, results in Mark and Moore (1987) indicate that slope-depth relationships among the main islands of the archipelago are, in general, similar.

Depth-stratified sampling

For the second phase of the assessment, each of the island areas was targeted for comprehensive trapping surveys to determine abundance patterns (i.e., catch rate) with depth and to estimate standing stocks (Table 1). A depth-stratified sampling approach was used. From preliminary data gathered at Kauai and Niihau during the September 1987 cruise, the mean and variance in CPUE were calculated for each of the six 92 m (50 fm) depth intervals lying in the 366–915 m (200–500 fm) range. Based on the results of this vertical distribution survey, sampling effort was optimally partitioned into depth strata by Neyman allocation (Cochran 1977), i.e., trap allocations to each depth interval were based on the product of abundance (CPUE · habitat area) and the standard deviation of CPUE at that depth. As each cruise progressed, CPUE means and variances were recalculated daily and the trap allocation schedule was updated.

From the results of the surveys, exploitable biomass was estimated (Eq. 1) for each depth interval at each site visited. This calculation assumes that the catchability estimate, which was determined at the depletion experiment study site, can be extended to all other localities sampled. An estimate of the variance of the biomass for each stratum was obtained from Eq. 1 using the delta method (Seber 1982), resulting in

$$\mathrm{VAR}[B] \approx \frac{A^2}{\hat{q}^2}\,\mathrm{VAR}[\mathrm{CPUE}] + \frac{A^2 \cdot \mathrm{CPUE}^2}{\hat{q}^4}\,\mathrm{VAR}[\hat{q}]$$

if all covariance terms are zero (a reasonable first assumption) and VAR[A] is negligible (see above). Confidence intervals were then calculated using the distribution of standard normal scores ($\alpha = 0.05$, $Z = 1.96$).

Length-frequency analysis

The Kaulakahi Channel experimental depletion site was visited on seven separate occasions during May 1986–March 1988 (Table 1). During each visit a length-frequency sample of *H. laevigatus* was obtained, with the ultimate goal of analyzing the progression of size modes over time (egg bearing is strongly seasonal; Dailey and Ralston 1986, Moffitt and Polovina 1987). Additional length-frequency samples were obtained during the course of the depth-stratified sampling at each of the island sites.

Mortality and growth parameters were estimated from length-frequency distributions using the regression method of Wetherall et al. (1987). This technique requires an equilibrium population size-structure, an undesirable and restrictive assumption. Even so, data are available to support its use. Dailey and Ralston (1986) present length-frequency data for male and female shrimp sampled during the earliest stages of the fishery (1983–84). The data are very similar to those presented here, suggesting that exploitation has yet to seriously affect size composition. Additionally, the time-invariance of the size-frequency data we collected at the Kaulakahi study site (see below) indicates equilibrium conditions.

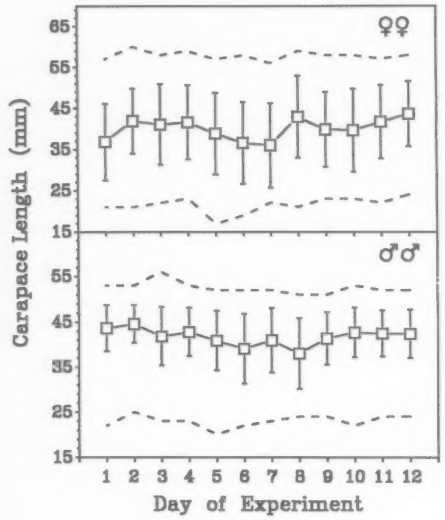

Figure 3

Distributions of carapace length for male and female *Heterocarpus laevigatus* during the depletion experiment. Open squares are means bracketed by ±1 SD; dashed lines represent maximum and minimum observed sizes.

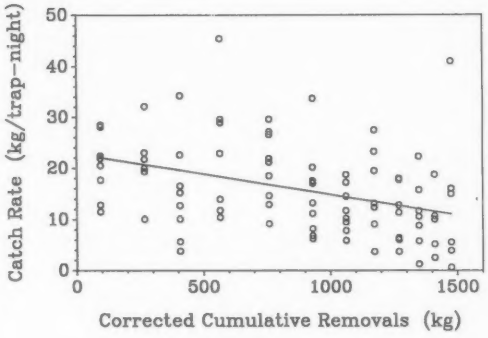

Figure 4

Leslie model applied to the experimental depletion of *Heterocarpus laevigatus* at the Kaulakahi Channel study site. Each point represents one valid trap-night of fishing.

For each sex, the von Bertalanffy asymptotic length (CL_∞) and the ratio (Θ) of the total mortality rate (Z/yr) to the von Bertalanffy growth coefficient (K/yr) were estimated from a weighted regression of mean lengths ($CL_{\mu i}$) on full vulnerability cutoff lengths (CL_{ci}). In the analysis, the CL_{ci} were incremented in 1.0 mm steps above CL_{co}, the minimum size of full vulnerability to the gear, and the $CL_{\mu i}$ were recalculated at each step. Using the morphometric functional regressions presented in Dailey and Ralston (1986), CL_{co} was set equal to 30 mm (the length of *H. laevigatus* with carapace width = 12.7 mm), corresponding to the least dimension of the wire mesh covering the traps. This approach to estimating CL_{co} deviates from that used in previous applications of the regression method to *H. laevigatus* stocks. Dailey and Ralston (1986) and Moffitt and Polovina (1987) both assumed that shrimp were not fully selected by baited traps until reaching a CL greater than the modal size of length-frequency distributions from trap catches.

Because the size-structure we observed was similar to the unexploited stock (see above), it follows that $\Theta = M/K$, where M is natural mortality/yr. Likewise, using the length-weight regressions of Dailey and Ralston (1986), we estimated the asymptotic weights (W_∞) for each sex as the predicted weight at $CL = CL_\infty$. The average size at entry to the fishery (CL_ρ, *sensu* Beverton and Holt 1957) was obtained by averaging the minimum size caught and CL_{co}. Given estimates of M/K, W_∞, and CL_ρ, we used the tables presented in Beverton and Holt (1966) to determine sex-specific values of yield-per-recruit (Y/R) at various levels of exploitation (F/M). From these data we computed values of $F_{0.1}/M$, the exploitation level at which the marginal increase in Y/R declines to 10% of its value at the origin (Gulland and Boerema 1973, Gulland 1983).

Results

Depletion experiment

During the depletion experiment, 123 pyramid shrimp traps were set at the Kaulakahi Channel study site. Of these, 19 were lost, resulting in 104 effective trap-nights of standard fishing effort and a gear loss rate of 15%. A total of 45,482 *H. laevigatus* were caught, which collectively weighed 1499 kg. The average size of each shrimp was therefore 33.0 g. During the 12-day course of the experiment, no change occurred in the daily mean size of shrimp caught (Fig. 3; $r_♀ = 0.32$, df 10; $r_♂ = -0.28$, df 10).

Individual trap catches were regressed on values of corrected cumulative removals to date (Fig. 4). Traps that did not fish properly (e.g., the funnel entrance was ajar upon retrieval) were not included, although cumulative removals (K_i) included all shrimp caught in the study area (<695 m or 380 fm). Therefore, each point represents an observation of CPUE from one valid

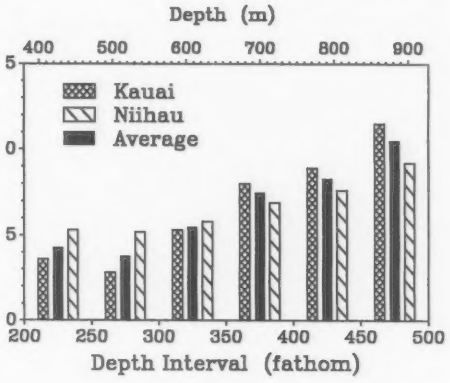

Figure 5
Distribution of habitat by depth at Kauai and Niihau. The composite average distribution is based on pooling habitat at these two sites.

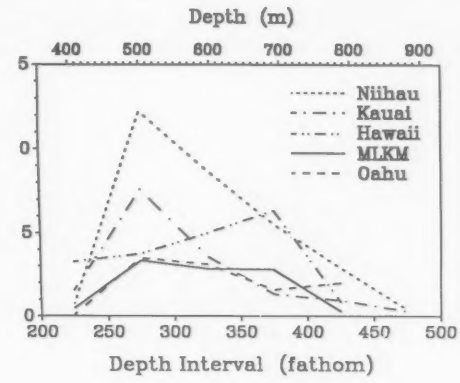

Figure 6
Average CPUE of *Heterocarpus laevigatus* relative to depth at each site sampled.

trap-night of fishing. Also presented is the ordinary least-squares regression equation relating these variables. The equation of the line is

$$CPUE_i = 22.84 - 0.007988[K_i],$$

with standard errors of the slope and intercept equal to 0.001997 and 1.9368, respectively. The regression is highly significant ($F_{1,89} = 16.00$, P 0.0001). The residuals show no obvious departure from linearity, an indication of constant catchability.

Under the Leslie model, the exploitable biomass at the start of the experiment is defined by the x-intercept, i.e., 2859 kg. Because the study site covered 1187 ha, this amounts to an initial density of 2.4087 kg/ha, which produced an initial catch rate ($CPUE_0$) equal to 22.84 kg/trap-night (i.e., the y-intercept). Then, $\hat{q}$ expressed on a hectare basis, rather than defined in terms of the study site, is estimated to be 9.4798 ha/trap-night. In real terms, one overnight soak of a single, large pyramidal shrimp trap is estimated to have captured ~0.8% of the shrimp in the entire study area, which is equivalent to all the shrimp in ~9.5 ha, were they randomly dispersed. The standard error of $\hat{q}$/ha is the product of A (1187 ha) and the standard error of $\hat{q}$ measured over the study site (0.001997) (Seber 1982).

It is instructive to note that an initial density of 2.4087 kg/ha is equivalent to an average of 73 shrimp/ha (see statistics for mean shrimp weight above). Based on this density, the average utilization of habitat by each shrimp was 137 m^2, a remarkable figure given the relatively high catch rate encountered at the beginning of the depletion experiment (22.83 kg/trap-night).

Depth-stratified sampling

Habitat areas by 92 m (50 fm) depth intervals were estimated for the Oahu, Hawaii, and MLKM sites by assuming that the proportionate distribution of habitat between 366 and 915 m (200–500 fm) at these sites was the same as the composite distribution obtained at Kauai and Niihau. While there were some differences in the distribution of habitat with depth between Kauai and Niihau (Fig. 5, Table 2), they were relatively minor. At both sites the amount of habitat in the 458–549 m (250–300 fm) depth interval was slightly less than in the 366–458 m (200–250 fm) interval; but with increasing depth below that, the amount of habitat per 92 m (50 fm) depth interval increased steadily.

There were, however, marked differences in CPUE with depth among the five localities sampled (Fig. 6, Table 2). Catch rates at Niihau were particularly high relative to the other areas, especially at 458–549 m (250–300 fm). Catch rates at Oahu and MLKM were much lower. The modes of the distributions at Kauai and Niihau were shifted to the shallow end of the depth range, whereas at Hawaii it was shifted deeper.

Results presented in Table 2 provide estimates of the exploitable biomass (B), as well as variance estimates, for the depth intervals sampled at each site. Although catch rates at Niihau are quite high, the reduced amount of habitat at this island (69,530 ha) is sufficient to support only a small stock of shrimp (35.7 MT). Oahu, with its much lower catch rates, has a larger exploit-

Table 2
Depth-stratified sampling results for *Heterocarpus laevigatus* in the main Hawaiian Is.

Depth range (m)	Depth range (fm)	No. traps set	Mean CPUE kg/trap	VAR[CPUE]	Habitat area (ha)	B (kg)	VAR[B]
Kauai							
366–458	200–250	29	1.566	0.894	12,760	2,108	1,897,271
458–549	250–300	37	7.587	1.093	12,070	9,663	7,608,356
549–640	300–350	25	3.607	0.322	14,410	5,481	2,621,353
640–732	350–400	18	1.324	0.436	16,940	2,367	1,742,930
732–824	400–450	6	0.953	0.203	17,770	1,786	912,472
824–915	450–500	7	0.299	0.038	20,200	637	197,960
Totals		122			94,150	22,042	14,980,342
Niihau							
366–458	200–250	9	0.788	0.586	10,670	887	791,140
458–549	250–300	18	12.214	7.253	10,570	13,611	20,586,349
549–640	300–350	19	8.719	3.335	11,010	10,127	10,907,759
640–732	350–400	10	5.533	2.737	11,730	6,847	7,120,644
732–824	400–450	4	2.903	0.906	12,210	3,739	2,377,052
824–915	450–500	4	0.380	0.094	13,340	535	204,092
Totals		64			69,530	35,746	41,987,037
Oahu							
366–458	200–250	6	0.122	0.017	41,570	535	342,588
458–549	250–300	20	3.482	3.239	40,100	14,726	71,490,061
549–640	300–350	33	3.115	0.480	45,070	14,810	24,568,526
640–732	350–400	13	1.594	0.698	50,800	8,542	24,613,230
732–824	400–450	2	1.990	0.303	53,300	11,187	17,379,858
824–915	450–500	0	0.000	0.000	59,510	0	0
Totals		74			290,350	49,800	138,394,264
Hawaii							
366–458	200–250	1	3.270	2.152	38,720	13,357	47,049,206
458–549	250–300	4	3.750	2.223	37,320	14,767	48,097,991
549–640	300–350	11	5.008	3.882	41,980	22,171	106,796,660
640–732	350–400	11	6.325	3.036	47,300	31,560	137,841,468
732–824	400–450	4	0.858	0.889	49,630	4,491	25,603,225
824–915	450–500	0	0.000	0.000	55,430	0	0
Totals		31			270,350	86,345	365,388,550
Maui–Lanai–Kahoolawe–Molokai							
366–458	200–250	15	0.500	0.110	69,420	3,662	6,716,452
458–549	250–300	43	3.338	0.399	66,920	23,567	54,580,681
549–640	300–350	42	2.823	0.168	75,250	22,409	41,983,921
640–732	350–400	19	2.795	0.653	84,790	25,004	91,353,003
732–824	400–450	1	0.300	0.079	88,970	2,815	7,443,949
824–915	450–500	0	0.000	0.000	99,370	0	0
Totals		120			484,730	77,457	202,078,006

able biomass of *H. laevigatus* than does Niihau. In aggregate, we estimate the exploitable stock at all islands to be $B_{\Sigma tot} = 271.4$ MT ($p[217.3 \leq B_{\Sigma tot} \leq 325.5] = 0.95$, SE 27.6 MT, CV 10.18%).

Analysis of length-frequency data

Although the Kaulakahi Channel study site was sampled on seven different occasions over a 29-month period (May 1986–October 1988), during which over 6800 female and 11,800 male shrimp were sexed and measured, there was little evidence of progression in size modes (Fig. 7). The CL frequency distributions of male shrimp were particularly stagnant, and those of females showed no coherent pattern that could be attributed to the influx of year-classes into the exploitable population.

Due to the apparent stationary behavior of these

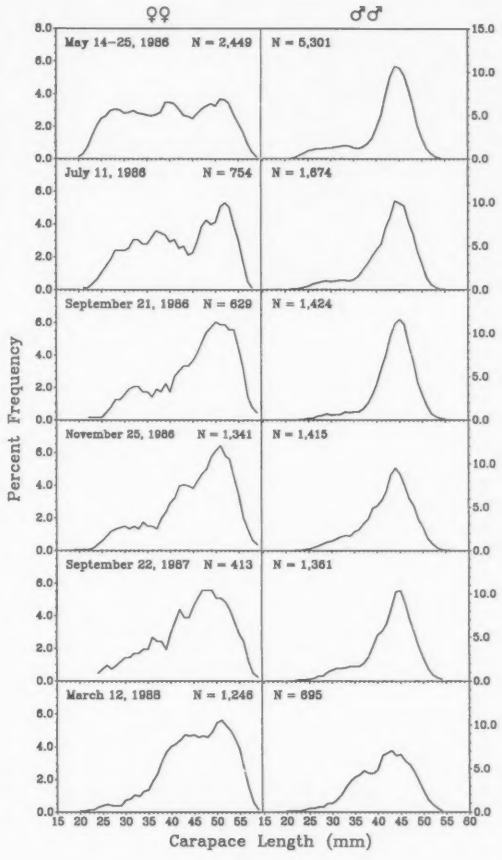

Figure 7
Length-frequency distributions of female and male *Heterocarpus laevigatus* at the Kaulakahi Channel study site.

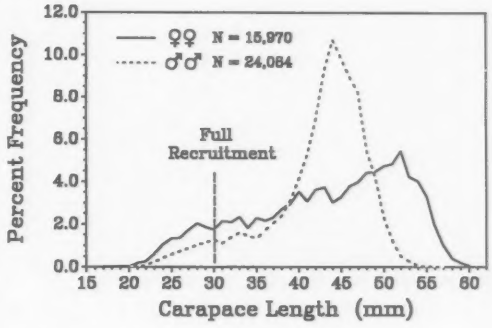

Figure 8
Composite length-frequency distributions for all female and male *Heterocarpus laevigatus* sampled.

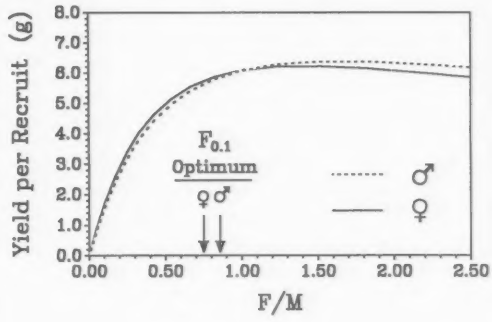

Figure 9
Yield-per-recruit of *Heterocarpus laevigatus* and estimates of optimum exploitation level ($F_{0.1}/M$).

distributions, all the length data were pooled (Fig. 8). It is evident from the figure that female shrimp reach substantially larger sizes than do males, in agreement with previously published work (Dailey and Ralston 1986, Moffitt and Polovina 1987). Superimposed on the combined length-frequency distributions of males and females is the estimated size of *H. laevigatus* when fully vulnerable to the traps (i.e., $CL_{co} = 30$ mm CL). The carapace width of shrimp this size is equal to 1.27 cm (0.5″), the minimum mesh size of the traps.

We applied the Wetherall et al. (1987) regression method to these length-frequency data and estimated that $\Theta_{♀} = 1.01 \pm 0.052$ and $\Theta_{♂} = 0.74 \pm 0.075$. For females we estimated that $CL_{\infty} = 58$ mm (SE 0.37) and for males $CL_{\infty} = 50$ mm (SE 0.44), corresponding to $W_{\infty} = 80$ g for females and 55 g for males.

The smallest shrimp we captured in the pyramid traps was 16 mm CL. Below this size, selectivity of the gear was zero. By equating carapace width and mesh size, we determined that $CL_{co} = 30$ mm. Thus, our estimate of the size at 50% recruitment to the fishery (CL_{r}) is 23 mm. Given this result, and sex-specific estimates of Θ and W_{∞}, we calculate that for females $F_{0.1}/M = 0.75$ and for males $F_{0.1}/M = 0.86$ (Fig. 9).

Discussion

In this assessment, projections of exploitable biomass depend greatly on the estimate of catchability obtained from the Leslie depletion experiment. Due to its major role in the calculations, sources of bias in its estimation must be considered carefully.

There is evidence to show that estimates of crustacean population size obtained through survey removal methods like the Leslie and DeLury methods (Ricker 1975) may severely misrepresent the actual size of the population. In his study, Morrissy (1975) found that DeLury estimates of population number of *Cherax tenuimanus* were anywhere from 39 to 53% of those based on a complete count of the population. Similarly, DeLury estimates of the population density of *Panulirus cygnus* were 25% of those estimated from diver counts (Morgan 1974a).

The most likely origin of bias in these situations is that not all individuals in the exploitable portion of the population are equally vulnerable (*sensu* Morrissy 1973) to the gear. For example, when sampling with baited drop nets, the catch of *C. tenuimanus* in intermolt, expressed as a known fraction of the actual population, was much higher than the catch in a premolt condition; individuals in molt stages immediately preceding and following ecdysis were not caught at all (Morrissy 1975).

It is possible that a similar bias was operating during the depletion study at the Kaulakahi Channel study site. The presence of shrimp in the exploitable portion of the population, which were less susceptible to trapping, would result in overestimation of catchability and underestimation of biomass. Factors such as molt stage (Morgan 1974b, Morrissy 1975), sex (Morrissy 1973), and feeding history (Sainte-Marie 1987) are known to cause variation in vulnerability to trapping. Although social dominance, mediated through differences in size, can affect catchability (Morrissy 1973, Chittleborough 1974), it is unlikely to have substantially biased our results because the catch size-structure remained unchanged during the experiment (Fig. 3). Also, Gooding et al. (1988) did not see "any overt aggressive behavior" among *H. ensifer* that were active around baits. Lastly, seasonal and interannual alterations in catchability due to temperature (Chittleborough 1970, Morgan 1974b), salinity (Morgan 1974b), and food availability (Chittleborough 1970) operate over longer time-scales than the depletion experiment.

Two other lines of evidence support the premise that shrimp biomass was underestimated. Although results presented in Figure 4 indicate that 12 days of trapping dropped the catch rate to 48% of its starting value (10.87 kg/trap-night), it had risen to 19.73 kg/trap-night when resampled 47 days later (data from 9–11 July 1986 cruise; see Table 1). If catchability is estimated from the decline in catch rate that occurred between the beginning of the depletion study (22.84 kg/trap-night) to the time the site was resampled 2 months later, and we assume the decline was due only to trap removals (1499.00 kg), we obtain $\hat{q} = 2.4624$ ha/trap-night. This represents a 74% reduction in the estimate, which in turn would inflate biomass estimates by a factor of 3.85 (i.e., $B_{\Sigma tot} = 1050$ MT). This relative bias is similar to that reported by Morgan (1974a) for *Panulirus cygnus* (see above).

From submersible observations of *H. laevigatus* density, Moffitt and Parrish (1992) obtained $\hat{q} = 0.2895$ ha/trap-night for the same traps we used, amounting to a 33-fold difference relative to our Leslie analysis. They, too, expressed concerns about bias in catchability estimates derived from depletion experiments due to variable susceptibility to the gear. Conversely, their estimate of catchability was based on comparing site-specific March 1988 trap catches with submersible observations made during August, even though *H. laevigatus* undergoes seasonal vertical migrations (King 1983, Dailey and Ralston 1986). In addition, at the start of each dive, they deployed a baited trap in the area of the submersible. Both factors could lead to underestimation of catchability.

It is clear that biased estimates of q will result if the probability of capture is not uniform among shrimp. In an attempt to solve this problem, Quinn (1987) developed a depletion model that explicitly incorporated a term for non-constant catchability. Application of his model to Pacific halibut effectively accounted for short-term trends in q, but auxiliary estimates of fishing and natural mortality were required, data that are unavailable here.

The primary objective of this study was to determine the exploitable biomass of *H. laevigatus* in the main Hawaiian Is. (MHI). Even if shrimp biomass were as high 1050 MT, rather than 271 MT (see above), our results indicate that the MHI stock is much smaller than previously believed, and that prior estimates of maximum sustainable yield (MSY) are much too high. For example, Struhsaker and Aasted (1974), using figures from a fishery for *H. reedi* off the coast of Chile, speculated that *H. ensifer* in Hawaii could sustain a level of production equal to 10–20 kg/ha $\cdot$ yr^{-1}. If *H. laevigatus* were assumed to be equally productive (e.g., Anon. 1979), then, given there are ~350,000 ha of prime habitat at 458–640 m (250–350 fm) in the MHI alone (Table 2), the resulting estimate of MSY exceeds stock biomass many times over. Moreover, catch rates of *H. laevigatus* in the distant Northwestern Hawaiian Is. (Nihoa to Kure), which represent a similar amount of shrimp habitat as the MHI, are no more than half those observed in the MHI (Gooding 1984, Tagami and Barrows 1988, Tagami and Ralston 1988).

Our estimates of $\Theta_{\varphi} = 1.01$ and $\Theta_{\sigma} = 0.74$ are much lower than those given in Dailey and Ralston (1986), who reported $\Theta_{\varphi} = 2.9$ and $\Theta_{\sigma} = 4.3$. By requiring CL_{∞} to be greater than the modal size, they effectively constrained Θ to values much greater than unity. A similar requirement was imposed by Moffitt and Polovina

(1987), who estimated $\Theta_{\varphi} = 1.9$ and $\Theta_{\sigma} = 2.1$ for *H. laevigatus* in the Mariana Is. Additionally, use of the "mode" criterion to establish the minimum size at full vulnerability results in substantially greater sensitivity of Θ to input estimates of CL_{co}. For example, if CL_{co} is 30 mm as we suggest (Fig. 8), ±2 mm perturbations in CL_{co} result in −9% and +12% changes in estimates of Θ_{σ}. However, if the mode of the size-frequency distribution is used instead ($CL_{co} = 44$ mm), the same perturbations alter estimates of Θ_{σ} by −16% and +46%. Similar sensitivity was observed in estimates of Θ_{φ}. In summary, it is our belief that independent estimates of CL_{co} are superior to those obtained from the size data analyzed, particularly when there is no reason to suspect that agonistic interactions affect the catch size-structure.

Lower values of Θ indicate a reduction in the instantaneous mortality rate (Z), an increase in the von Bertalanffy growth coefficient (K), or both. We favor the first hypothesis, largely because of the cold (4–6°C), trophically-impoverished habitat in which *H. laevigatus* reside. In many respects these shrimp represent a crustacean analog to Pacific ocean perch *Sebastes alutus*, which grow very slowly, exhibit extreme longevity, and display low rates of natural mortality (Leaman and Beamish 1984). Consequences of this life-history pattern are that (1) under pristine conditions, individuals accumulate in the largest size-categories (Fig. 8), (2) the ratio of production to biomass is low, and (3) stocks are very susceptible to overfishing.

Acknowledgments

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Interannual variation and overlap in the diets of pelagic juvenile rockfish (Genus: *Sebastes*) off central California

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Abstract.–The diets of pelagic juveniles of widow rockfish *Sebastes entomelas*, yellowtail rockfish *S. flavidus*, chilipepper *S. goodei*, shortbelly rockfish *S. jordani*, and bocaccio *S. paucispinis* were compared using samples collected during 1984–87. All five species co-occur as pelagic juveniles off central California. Frequency of occurrence, percent by number, and a ranking index of prey items were determined from 1088 stomachs. Major prey of pelagic juvenile rockfish were the various life stages of calanoid copepods and subadult euphausiids (including eggs).

For each year, dietary overlap was quantified between interspecific pairs using the Colwell and Futuyma (1971) index. Amount of overlap varied from year to year. Long-term intraspecific dietary overlap, based on the 4 years of data, was generally less than interspecific overlap within years. Year-to-year variation in the diets of these species was generally greater than within-year variation among them, suggesting that, as a group, pelagic juvenile rockfishes are opportunistic feeders. Also, if interannual variation in the distribution and abundance of foods has a major impact on recruitment, the high dietary overlaps of these co-occurring species would suggest parallel survival and year-class success.

Multivariate analysis of variance was used to examine the effects of latitude, depth, and fish size on food consumption. Alterations in diet were related to latitude, depth, and a latitude-depth interaction for three species in 1987 and, also, for shortbelly rockfish in 1984–86. Diet was apparently unrelated to fish size.

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Fishery Bulletin, U.S. 90:505–515 (1992).

Rockfishes of the genus *Sebastes* are a major component of the west coast groundfish fishery (Gunderson and Sample 1980), yet little is known of their early life history. Kendall and Lenarz (1987) noted a particular lack of information on the biology of the pelagic juvenile life-stage. To date most work on pelagic juveniles has addressed problems in identification (e.g., Moser et al. 1977, Laroche and Richardson 1980 and 1981, Matarese et al. 1989), growth (Boehlert 1981a, Boehlert and Yoklavich 1983, Penney and Evans 1985, Laidig et al. 1991, Woodbury and Ralston 1991), and vertical distribution (Boehlert 1977 and 1981b, Moser and Alhstrom 1978, Moser and Boehlert 1991, Lenarz et al. 1991).

Female rockfishes undergo internal fertilization and the eggs develop within the ovary for a 40–50 day period (Kendall and Lenarz 1987). Larvae hatch internally, are extruded approximately 1 week later, and begin feeding. Larvae grow and transform into juveniles, a developmental stage characterized by the attainment of full meristic characters. Many rockfishes have a pelagic juvenile stage. Pelagic juveniles ranging in size from 15–100 mm SL are abundant off central California from April to June, although distributional patterns vary markedly among species and years (Wyllie Echeverria et al. 1990). The pelagic juvenile stage ends with settlement into demersal or nearshore habitats.

Evidence strongly indicates that the recruitment of marine fishes is heavily influenced by events that occur early in the life history (Blaxter 1974). A frequently proposed explanation is that the availability and abundance of foods appropriate for first-feeding larval and later juvenile stages are critical to adequate survival and growth. A reduction in the fine-scale density of suitable prey items, whether due to an absolute decrease in prey abundance (Hjort 1914) or to a randomized dispersion of what formerly was a patchy prey resource (Lasker 1975), can have a negative impact on survival. Reduced prey densities can affect survivorship directly through starvation, or indirectly by reducing growth rates and thereby prolonging exposure to other size-specific mortality factors

(e.g., predation, advection, etc.). Regardless of the mechanism, variation in the availability of food can have a major effect on year-class strength (Lasker 1981). The study of food utilization patterns and diet overlap is, therefore, useful in understanding survival mechanisms during the pelagic juvenile life stage. Moreover, annual variation in the extent of interspecific dietary overlap may indicate changes in the distribution and abundance of prey (e.g., Zaret and Rand 1971). Since this may well be critical in determining the success of a year-class, similarity in food habits among pelagic juvenile rockfish may result in similar recruitment dynamics.

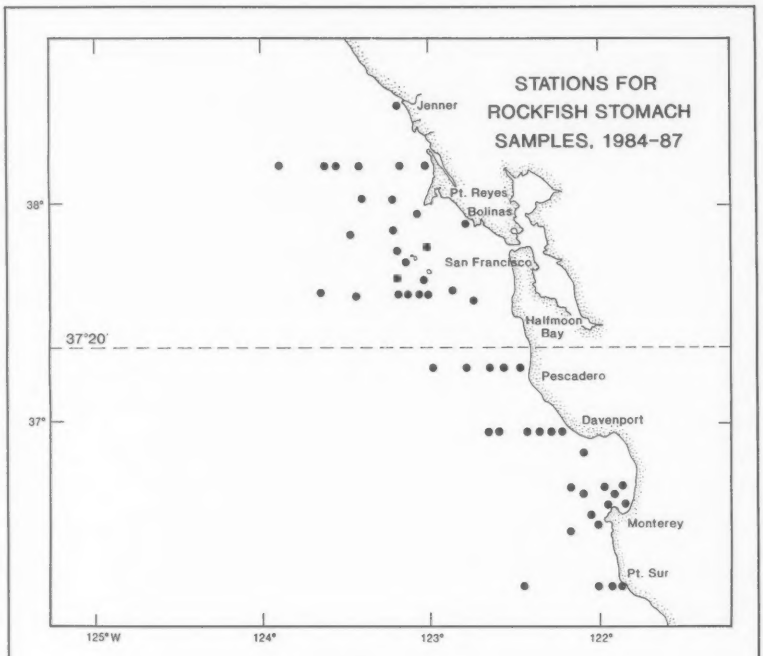

Figure 1
Map of the central California coast showing locations of midwater trawl stations where *Sebastes* stomach samples were obtained, 1984–87.

Previous published dietary studies of juvenile rockfish have been limited to (1) experimental work on food ration and growth in black rockfish (*S. melanops*, Boehlert and Yoklavich 1983); (2) a description of the diet of newly settled Pacific ocean perch (*S. alutus*, Carlson and Haight 1976); (3) a comparison of the food habits of seven *Sebastes* spp. in a nearshore kelp-forest habitat (Singer 1985); and (4) predation on barnacle larvae by a mixed assemblage of settled kelp resident juvenile rockfishes (Gaines and Roughgarden 1987). The purpose of this study was to examine the feeding ecology of several co-occurring young-of-the-year pelagic juvenile rockfishes, including widow rockfish *S. entomelas*, yellowtail rockfish *S. flavidus*, chilipepper *S. goodei*, shortbelly rockfish *S. jordani*, and bocaccio *S. paucispinis*. Specific goals of this study were to (1) identify the food habits of these five species during the pelagic juvenile stage, (2) determine the extent of dietary overlap among the five species, and (3) determine the degree of interannual variation in patterns of prey utilization.

Materials and methods

Juvenile rockfish used in this study were obtained from midwater trawl samples made during a series of annual pelagic juvenile rockfish surveys conducted off central California during 1984–87. Details of these surveys are described in Wyllie Echeverria et al. (1990). The primary purpose of the surveys was to estimate the distribution and abundance of the pelagic-stage juveniles of age-0 rockfishes. Survey areas and dates differed somewhat from year to year (Fig. 1, Table 1). The surveys were conducted during June, except in 1987 when the survey extended from late-May to June. In 1984 and 1985, the survey area extended from Point Sur (lat. 36°18′N) to Point Cabrillo (lat. 39°20′N). Bottom depths at each trawl station ranged from <50 m at nearshore localities to >3700 m beyond the continental shelf. The sampling plan was revised in 1986; seven transects composed of 36 stations were selected based on previous records of rockfish abundance and the availability of ship time. These stations were sampled repetitively during three consecutive sweeps of the area. After 1985, the survey area extended from Cypress Point (lat. 36°35′N) to Point Reyes (lat. 38° 00′N), with station depths ranging from <50 to 1000 m.

Collections were made from the RV *David Starr Jordan* with a modified Cobb midwater trawl net having a 24.4 m head rope and 0.76 cm mesh liner in the cod-end. The standard depth sampled was 30 m. However, at shallow stations (bottom depth <100 m) the net was set at 5–10 m. At some deep stations samples were

Table 1
Number of juvenile *Sebastes* stomachs examined from juvenile rockfish surveys, 1984–87.

Year	Survey dates	Species	No. of stomachs	Range (mm SL)
1984	8–24 June	Widow rockfish	15	40–63
		Yellowtail rockfish	40	36–56
		Chilipepper	20	38–55
		Shortbelly rockfish	120	30–65
		Bocaccio	50	21–77
1985	5–30 June	Widow rockfish	75	43–63
		Yellowtail rockfish	30	39–48
		Shortbelly rockfish	85	49–75
1986	3–25 June	Yellowtail rockfish	10	35–47
		Shortbelly rockfish	168	15–47
		Bocaccio	25	18–40
1987	23 May–21 June	Widow rockfish	105	48–80
		Yellowtail rockfish	17	39–52
		Chilipepper	125	41–76
		Shortbelly rockfish	150	17–78
		Bocaccio	53	22–86
Total stomachs examined			1088	

also collected at 100 m. Nets were fished for 15 min at depth during the night, ~30 min after sunset, or before sunrise.

Five specimens of each species were randomly subsampled from each haul for dietary analysis. Generally, no samples were taken if fewer than five individuals were taken in a haul. Specimens were tentatively identified to species and preserved whole in 10% buffered formalin, usually within 1 hour of collection. Identifications were later verified ashore with meristics keys (Matarese et al. 1989, Moreland and Reilly 1991); samples were transferred to 70% isopropyl alcohol within 1 month of collection. Standard length (SL) was later measured to the nearest 0.1 mm. Stomachs were removed and stored in 70% isopropyl alcohol until examined.

Stomach contents were examined with a dissecting microscope. Empty stomachs were noted and the digestive state of each prey item was coded on a scale of 1–3, with 3 representing digestion too advanced for identification. All prey types were identified to the lowest possible taxonomic level and counted. When possible, a subsample of all prey types was measured along the longest axis with an ocular micrometer. Heads or eyes were used to obtain total counts when food items were fragmented. For each rockfish species, the proportion of prey types in the diet was calculated as the percentage of total prey numbers consumed in a year, summed over all the individuals examined for stomach contents.

A ranking index, modified from Hobson (1974), was calculated for the major food items. The index (I_r) is the product of proportional frequency of occurrence and percent by number, calculated for all specimens of a species in a year. To quantify dietary overlap among species, the index of Colwell and Futuyma (1971) was used, that is,

$$C_{ih} = 1.0 - 0.5 \left(\sum_{j=1}^{n} p_{ij} - p_{hj} \right),$$

where p_{ij} and p_{hi} are the numerical proportions of prey $j = 1 \ldots N$ found in the diets of species i and h, respectively. The index has a minimum value of zero, when no overlap occurs, and a maximum value of one, when all prey are shared in equal proportions by the two species.

Multivariate analysis of variance (MANOVA) was used to examine relationships among latitude, bottom depth, and the diets of chilipepper, shortbelly, and widow rockfish (Green 1978, SAS 1985). Although only in 1987 were there sufficient data to analyze the diets of all three species, adequate samples of shortbelly rockfish were obtained during all years (1984–87). Thus, examination of overall variation in diet through time, vis-à-vis latitude and depth, was limited to shortbelly rockfish. Analyses were confined to the three prey types of highest frequency of occurrence during the year examined, which varied among the different species and years. The numerical proportions of the three prey types (the dependent variables) were arcsine-transformed (Sokal and Rohlf 1981) prior to MANOVA testing. Latitude, depth, and a latitude-depth interaction term were the independent variables. Station latitude was classified as either north or south of lat. 37°20'N. Similarly, station depth was divided into deep (>100 m) or shallow (<100 m) categories. Data for chilipepper, shortbelly, and widow rockfish sampled in 1987 were also divided into large (>1987 median SL) and small (<1987 median SL) size-classes to examine diet variation as a function of fish size. Shortbelly rockfish were sufficiently numerous during all years to analyze diet variation as a function of predator size. Prey types for this analysis were again limited to the three prey categories with the highest overall frequencies of occurrence in a year, and the dependent variables were the arcsine-transformed numerical proportions in the diet.

Table 2

Summary of stomach contents for five species of pelagic juvenile *Sebastes*, 1984. FO = frequency of occurrence; % = percent by number.

	Widow rockfish (*n* 15)		Yellowtail rockfish (*n* 40)		Chilipepper (*n* 20)		Shortbelly rockfish (*n* 120)		Bocaccio (*n* 50)	
Prey category	FO	%	FO	%	FO	%	FO	%	FO	%
EUPHAUSIACEA										
Furcilia	33.3	10.1	50.0	12.3	30.0	6.8	54.2	35.1	36.0	24.1
Calyptopis			2.5	0.3			1.0	0.1	2.0	0.2
Juveniles	20.0	3.2	15.0	3.4	15.0	2.6	14.1	10.2	38.0	25.3
AMPHIPODA										
Hyperiid juveniles							1.0	0.1	4.0	0.3
CUMACEA							1.7	0.1		
DECAPODA										
Natantia juveniles	6.7	0.5					1.0	0.2		
COPEPODA										
Calanus spp.	46.7	41.0	52.5	28.7	40.0	27.2	40.8	15.1	34.0	31.6
Candacia sp.			5.0	0.4			6.7	0.5	2.0	0.2
Copepods (unidentified)	26.7	17.6	47.5	14.7	15.0	10.5	36.7	12.0	30.0	15.8
Juveniles	20.0	27.7	17.5	40.2	40.0	52.9	10.8	26.8	2.0	0.9
OSTEICHTHYES										
Fish larvae (unidentified)									20.0	1.7

Results

Frequency of occurrence and percent number

Stomachs from 1088 pelagic juvenile rockfish collected from midwater trawls during the four survey years (Table 1) were examined. Frequency of occurrence and percent number for specific prey types of each rockfish species varied considerably from year to year (Tables 2–5). In 1984, bocaccio differed from all other rockfish species in the frequency of occurrence of fish larvae as a prey type (Table 2). Euphausiid eggs occurred in the stomachs of all three species in 1985, although there is a disparity in the percent number (Table 3). Euphausiid eggs were much less frequent in the diets of the three rockfish species in 1986 (Table 4), whereas juvenile euphausiids occurred more frequently. Overall, data from 1984–87 show that prey items having a high frequency of occurrence generally had a high percentage by number. Euphausiid eggs and juveniles and unidentified copepods often had high percentages by number relative to their frequencies of

Table 3

Summary of stomach contents for three species of pelagic juvenile *Sebastes*, 1985. FO = frequency of occurrence; % = percent by number.

	Widow rockfish (*n* 75)		Yellowtail rockfish (*n* 30)		Shortbelly rockfish (*n* 85)	
Prey category	FO	%	FO	%	FO	%
EUPHAUSIACEA						
Furcilia	22.7	1.7	30.0	1.2	14.1	0.4
Calyptopis	2.7	0.1	6.7	1.5	1.2	0.1
Juveniles	5.3	0.7	10.0	0.2	16.5	0.4
Euphausiid eggs	18.7	8.2	36.7	59.1	48.2	59.3
AMPHIPODA						
Hyperiid juveniles	6.7	0.1	3.3	0.1	7.1	0.1
LARVACEA	6.7	4.1			7.1	2.4
CHAETOGNATHA	1.3	0.1				
DECAPODA						
Natantia juveniles			3.3	0.1	1.2	0.1
COPEPODA						
Calanus spp.	22.7	1.7	16.7	1.2	25.9	1.2
Candacia sp.	2.7	0.1	3.3	0.1	1.2	0.1
Copepods (unidentified)	13.3	3.7			17.6	2.9
Eucalanus sp.	8.0	1.8			3.5	0.1
Euchirella sp.	2.7	0.2			3.5	0.1
Juveniles	44.0	77.6	56.7	36.5	57.6	33.3
Metridia sp.			3.3	0.1	1.2	0.1
OSTEICHTHYES						
Fish larvae (unidentified)	1.3	0.1				

Table 4

Summary of stomach contents for three species of pelagic juvenile *Sebastes*, 1986. FO = frequency of occurrence; % = percent by number.

	Yellowtail rockfish (*n* 10)		Shortbelly rockfish (*n* 168)		Bocaccio (*n* 25)	
Prey category	FO	%	FO	%	FO	%
EUPHAUSIACEA						
Furcilia	10.0	1.6	13.2	0.9	4.0	0.2
Calyptopis	10.0	0.6	3.6	0.1		
Juveniles	70.0	7.1	59.9	10.0	52.0	22.0
Euphausiid eggs			4.8	1.1		
CUMACEA	10.0	1.0	1.2	0.1		
DECAPODA						
Natantia juveniles	20.0	1.0	0.6	0.1		
COPEPODA						
Calanus spp.			38.3	6.6	64.0	30.5
Copepods (unidentified)			34.1	3.9	28.0	5.9
Epilabidocera sp.	40.0	8.7				
Juveniles	50.0	80.1	71.9	77.3	44.0	41.4

occurrence. Euphausiid eggs and juvenile copepods were the smallest significant prey of pelagic juvenile rockfish. It is therefore not surprising that these categories often display high percentages by number. Likewise, the category 'unidentified copepods' typically was based on counts of small items (e.g., head fragments).

Ranking index

Prey having both a high frequency of occurrence and percentage by number are the most important items in the diet (Tables 2–5). *Calanus* spp. copepods were particularly important in 1984 when all rockfish species consumed substantial numbers of this

Table 5

Summary of stomach contents for five species of pelagic juvenile *Sebastes*, 1987. FO = frequency of occurrence; % = percent by number.

	Widow rockfish (*n* 105)		Yellowtail rockfish (*n* 17)		Chilipepper (*n* 125)		Shortbelly rockfish (*n* 150)		Bocaccio (*n* 53)	
Prey category	FO	%	FO	%	FO	%	FO	%	FO	%
EUPHAUSIACEA										
Furcilia	6.6	0.20	11.8	1.1	8.0	1.30	40.7	4.00	1.9	0.1
Calyptopis	8.5	0.30	5.9	0.4	2.4	0.40	6.7	1.60	1.9	0.1
Juveniles	39.6	9.00	76.5	31.1	19.8	10.30	6.7	0.60	30.2	10.7
Euphausiid eggs	27.4	52.00	5.9	7.7	10.4	35.80	28.7	65.80	1.9	10.5
Euphausiids (unidentified)	8.5	0.30	5.9	0.2	8.0	0.60	8.0	0.20		
Euphausia sp.									3.8	0.2
Thysanoessa sp.	1.0	0.01								
AMPHIPODA										
Hyperiids	1.0	0.01			1.6	0.10	1.0	0.01	1.9	0.1
CUMACEA					1.0	0.04				
DECAPODA										
Natantia juveniles	1.0	0.04			1.0	0.04				
Crab megalopa					3.2	0.20				
Crab zoea					1.6	0.10	1.0	0.01		
CIRRIPEDIA										
Cypris larva							1.0	0.10		
COPEPODA										
Calanus spp.	33.0	19.80	47.1	13.9	28.0	22.80	44.0	20.30	32.1	11.5
Candacia sp.					1.0	0.10			1.9	0.2
Copepods (unidentified)	22.6	7.30	5.9	1.1	8.0	4.10	4.0	1.00	13.2	45.8
Eucalanus sp.	1.9	0.10							1.9	0.1
Euchaeta sp.									1.9	0.8
Rhincalanus sp.	1.0	0.01					1.0	0.01		
Juveniles	24.5	10.00	17.7	44.5	14.4	24.30	16.0	6.30	5.7	19.3
TEUTHOIDEA										
Squid larva									1.9	0.1
OSTEICHTHYES										
Fish larvae									15.1	0.6
Eggs	3.8	1.00					2.0	0.40		

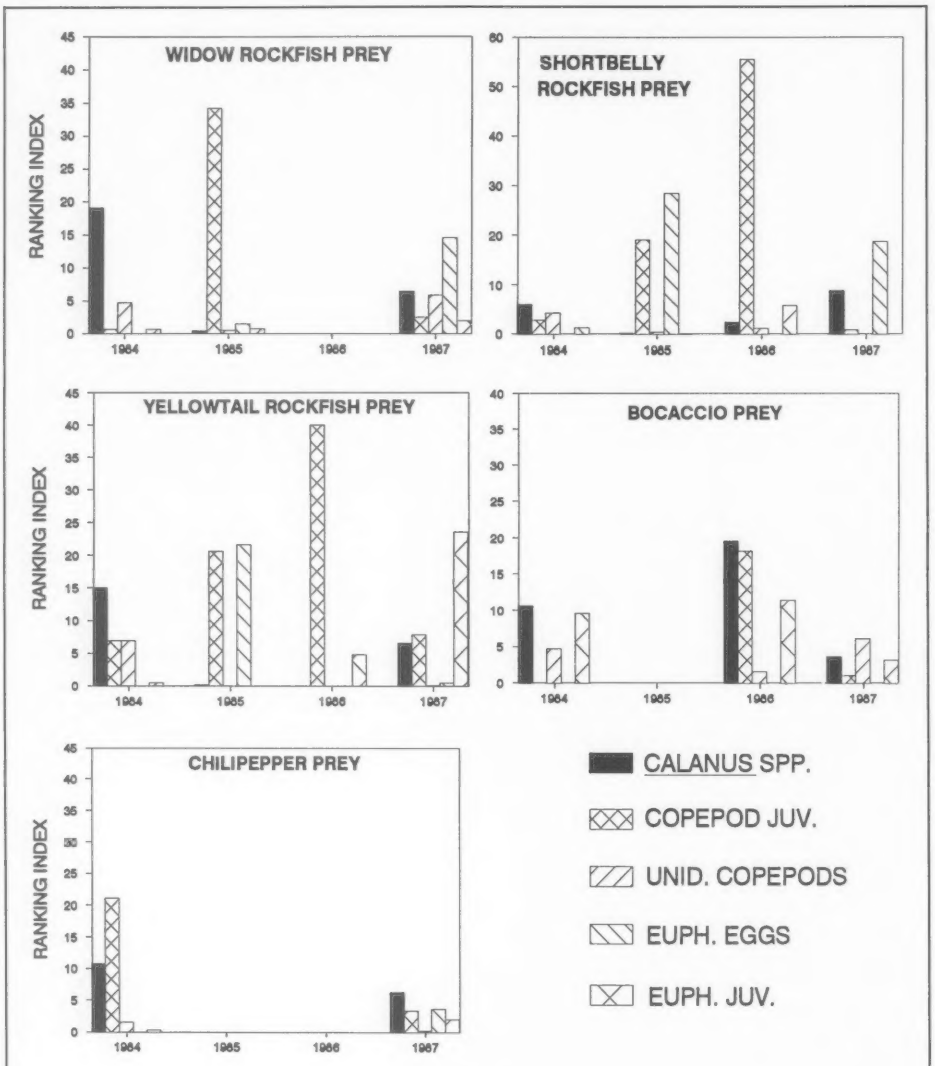

Figure 2

Histograms of the prey ranking index across years for five species of pelagic juvenile *Sebastes*. *Calanus* spp. = *Calanus* spp. copopods; copepod juv. = copopod juveniles; unid. copepods = unidentified copepods; euph. eggs = euphausiid eggs; euph. juv. = euphausiid juveniles.

prey. Likewise, 1985 was a year in which copepod juveniles and euphausiid eggs dominated the diets of the three species examined (widow, yellowtail, and shortbelly rockfish) and copepod juveniles were again important to all species in 1986.

Interspecific prey utilization patterns were less obvious. There is some indication that widow and chilipepper rockfish consumed more copepod juveniles and *Calanus* spp. copepods than did the other species. Similarly, shortbelly rockfish appeared to consume more euphausiid eggs, while bocaccio consumed more euphausiid juveniles. Likewise, there was some suggestion that bocaccio fed on larger prey than the other species (e.g., euphausiid adults and fish larvae). Nonetheless, no distinctive separation in primary prey species was evident among the five species examined.

Based on the I_r ranking index, it is apparent that the diet of pelagic juveniles is typically dominated by

a single prey type each year, followed by several prey types with indices at much lower values (Fig. 2). There were few instances in which the two most important prey types were similar in ranking index, e.g., yellowtail rockfish consuming euphausiid eggs (21.7) and juvenile copepods (20.7) in 1985. This result suggests that each year these species, to a large extent, specialize on foods that are intermittently abundant. Also, the ranking index data, together with information on frequency of occurrence and percent by number, indicate the major prey items of pelagic juvenile rockfish were various life stages of copepods and subadult euphausiids.

Dietary overlap

The extent of interspecific dietary similarity was quantified by comparing dietary overlaps among ali possible pairs of species within each year (1984–87). Ten species pairs were possible, but not all pairs were observed each year since all five species were not always collected (Table 6). Overlap indices are sensitive to the taxonomic level to which prey items are categorized; thus, statistical tests of significance concerning the data are arbitrary. Therefore, the convention established by Langton (1982) and Brodeur and Pearcy (1984) was invoked. Overlap index values of 0.00–0.29 were considered low, values of 0.30–0.60 were considered medium, and values >0.60 were considered high.

Using these criteria, annual comparisons of the distribution of overlap indices for 1984 indicate that 60% of all comparisons were classified as medium and 40% were classified as high. Results from 1985 and 1986 indicate that 67% of the scores were medium and 33% were high. In contrast, index values during 1987 generally had the lowest amount of overlap: 10% low, 70% medium, and 20% high. Based on these findings we conclude that, although overall patterns of dietary overlap do vary from one year to the next, variations are relatively modest (only in 1987 was any low overlap observed). Moreover, in this study most within-year species pairings showed >30% overlap. The principal exception to this generalization was for yellowtail and shortbelly rockfish sampled in 1987. Their diets were quite dissimilar.

Overlap indices were also calculated for all possible interannual intraspecific combinations. These calculations allow an assessment of the temporal stability of the diet relative to the amount of interspecific dietary overlap displayed during a given year. The frequency distribution of dietary overlap values derived from self-pairing of rockfish species from different years is shifted well to the left (toward zero) of the distribution of interspecific scores obtained within a year (Fig. 3). These findings show that in any particular year the different species of rockfish are opportunistic feeders that utilize relatively similar prey items, but substantial dietary change can occur from year to year.

Table 6

Diet overlap indices for individual pairings of pelagic juvenile *Sebastes* (1984–87). Wid = widow rockfish; Yel = yellowtail rockfish; Chi = chilipepper; Sho = shortbelly rockfish; Boc = bocaccio.

	Year			
Species pair	1984	1985	1986	1987
Wid–Yel	0.84	0.53	—	0.39
Wid–Chi	0.58	—	—	0.69
Wid–Sho	0.52	0.46	—	0.77
Wid–Boc	0.57	—	—	0.50
Yel–Chi	0.61	—	—	0.52
Yel–Sho	0.58	0.90	0.91	0.22
Yel–Boc	0.64	—	0.46	0.48
Chi–Sho	0.38	—	—	0.56
Chi–Boc	0.41	—	—	0.49
Sho–Boc	0.61	—	0.51	0.30

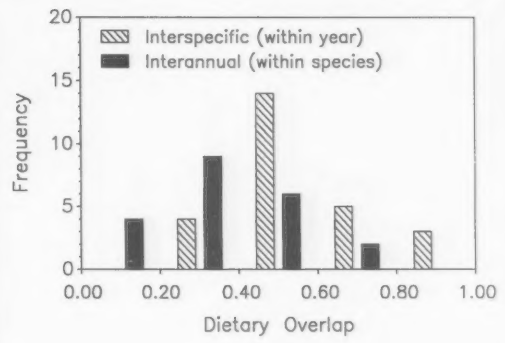

Figure 3

Frequency of dietary overlap indices among all interspecific *Sebastes* pairs within years, compared with frequency of overlap indices calculated for each *Sebastes* species self-paired across years.

Latitude and depth effects

Dietary variation with respect to station latitude (north or south of lat. 37°20′N), station depth (deeper or shallower than 100 m), and the interaction of these variables were analyzed using MANOVA (Table 7). The statistical significance of each analysis depended on the particular combination of species and year examined. In 1987, highly significant ($P<0.001$) diet variations occurred with depth for shortbelly and widow rockfish.

Table 7

Results of MANOVA of depth, latitude, and depth by latitude effects on three principal prey types of pelagic juvenile *Sebastes*. Cal = *Calanus* spp.; CoJv = copepod juveniles; EJv = euphausiid juveniles; EuEg = euphausiid eggs; ELv = euphausiid larvae; UnCo = unidentified copepods; Fur = furcilia.

					MANOVA model effects					
		Prey type			Depth		Latitude		Depth * latitude	
Species	Year	I	II	III	Wilks' λ	*P*	Wilks' λ	*P*	Wilks' λ	*P*
Chilipepper	87	Cal	CoJv	EJv	0.9019	0.0580[b]	0.9186	0.1044	0.9715	0.5525
Widow	87	Cal	EuEg	EJv	0.6638	0.0001**	0.9536	0.2813	0.9805	0.6632
Shortbelly	87	Cal	EuEg	ELv	0.7649	0.0001**	0.9805	0.5059	0.9243	0.0252*
Shortbelly	86	Cal	CoJv	EJv	0.8917	0.0005**	0.7522	0.0001**	0.9404	0.0234*
Shortbelly	85	Cal	EuEg	CoJv	0.8934	0.0472*	0.9293	0.1600	0.9185	0.1121
Shortbelly	84	Cal	UnCo	Fur	0.9647	0.3110	0.9213	0.0429*	0.9095	0.0240*

Significance levels:
[b]borderline
*$P<0.05$
**$P<0.01$

In that year, latitude had no discernible influence on the diet of these two species, although for shortbelly rockfish a significant interaction between depth and latitude was evident. These findings strongly suggest that spatial variability in the environment (i.e., latitude and depth of the water column) can influence, to some extent, the diets of pelagic juvenile rockfish in a species-specific manner.

Results for the full time-series of shortbelly rockfish data (1984–87) also show that spatial patterns change over time. Although depth had a highly significant effect on diet in 1986 and 1987, it was not significant in 1984 or 1985. Similarly, latitude had no appreciable relationship to the diet of shortbelly rockfish in 1985 and 1987, but it had a highly significant effect in 1986. Importantly, whenever a latitude correlation with diet was present, the interaction term (depth * latitude) was significant as well. We believe that the erratic influence of spatial structure on the shortbelly diet is likely due to the dynamic nature of the nearshore pelagic/neritic physical environment.

Using the 1987 data, we examined the least-squares means (Searle et al. 1980) of the transformed numerical proportions of the individual prey types to learn exactly how dietary composition varied when statistically-significant model effects occurred. In that year, the diet of chilipepper showed borderline significance with depth ($P = 0.058$); the least-squares means revealed that chilipepper consumed more *Calanus* spp. copepods in shallow water, and more juvenile copepods and juvenile euphausiids at bottom depths >100 m. Likewise, all three prey types (*Calanus* spp., euphausiid eggs, and juvenile euphausiids) of widow rockfish were consumed in greater proportion in deep water, especially euphausiid eggs. For shortbelly rockfish, which displayed a significant interaction term, consumption of *Calanus* spp. copepods was noticeably depressed at shallow southern stations. Euphausiid eggs were consumed in much greater quantities at deep stations, both north and south, while fewer larval euphausiids (furcilia and calyptopis) were found in fish from northern deep stations.

Predator size

Results were inconsistent when these same data (i.e., numerical proportions in the diet of the three most frequently occurring prey items for 1984–87 shortbelly rockfish, 1987 chilipepper, and 1987 widow rockfish) were also explored with MANOVA to assess the effect of fish size on composition of the diet. In each instance, fish were assigned to either small or large size-classes, based on whether standard lengths were smaller or larger than the annual median of that species.

Of the six cases examined (Table 8) two yielded significant ($P<0.05$) results. Large shortbelly rockfish sampled in 1986 tended to eat a higher proportion of *Calanus* spp. copepods, whereas small fish had a higher fraction of juvenile euphausiids and juvenile copepods in their diet. Results from that year, therefore, support the view that large fish tend to consume large prey. Even so, a significant size effect was demonstrated for 1985 shortbelly rockfish, which was exactly the opposite of 1986; large fish consumed fewer *Calanus* spp. copepods and a greater percentage of euphausiid eggs than did small fish. Sample size was not adequate to statistically analyze fish length jointly with distributional patterns. However, in 1985, 34 of

Table 8

Results of MANOVA of fish size on three principal prey types of pelagic juvenile *Sebastes*. Cal = *Calanus* spp.; CoJv = copepod juveniles; EJv = euphausiid juveniles; EuEg = euphausiid eggs; ELv = euphausiid larvae; UnCo = unidentified copepods; Fur = furcilia.

		Prey type			Fish size	
Species	Year	I	II	III	Wilks' λ	P
Chilipepper	87	Cal	CoJv	EJv	0.9927	0.9088
Widow	87	Cal	EuEg	EJv	0.9678	0.4407
Shortbelly	87	Cal	EuEg	ELv	0.9634	0.2132
Shortbelly	86	Cal	CoJv	EJv	0.9362	0.0161*
Shortbelly	85	Cal	EuEg	CoJv	0.8801	0.0261*
Shortbelly	84	Cal	UnCo	Fur	0.9928	0.8654

*$P<0.05$

the 42 shortbelly rockfish that were classified as small came from deep stations. Results presented earlier (Table 7) showed that the diet of shortbelly rockfish varied significantly with depth in 1985 (i.e., fewer euphausiid eggs and copepod juveniles at deep stations). Thus, the conclusion that small fish consumed large prey in 1985 is, to some degree, confounded with this spatial effect.

Discussion

The five species of pelagic juvenile rockfish examined in this study consumed pelagic zooplankton almost exclusively. Relatively few prey types made up the major portion of the diet each year. Various life history stages of calanoid copepods and euphausiids dominated. Carlson and Haight (1976) reported that copepods and euphausiids were important in the diet of pelagic juvenile Pacific ocean perch *S. alutus*. Singer (1985) recently reported that settled juveniles of several rockfish species consumed copepods and zoea larvae in a central California kelp forest. Other studies (Robb and Hislop 1980, Bowman 1981, Conway 1980) have also demonstrated that calanoid copepods and euphausiids are extremely important foods to pelagic juvenile fishes in the northeastern Pacific Ocean. These studies demonstrate that the diets of pelagic juvenile rockfishes are similar to those of other species possessing pelagic juvenile life stages.

A significant finding of this study is that *Sebastes* spp. juveniles periodically forage heavily on euphausiid eggs. Euphausiid eggs have not been previously reported as a prey item of pelagic juvenile rockfish and yet they were a very important dietary component both in 1985 and 1987. During those years, euphausiid eggs averaged over 37% of the prey items consumed by the five species studied. However, euphausiid eggs were absent from samples collected in 1984 and were a minor component in 1986.

Some species of euphausiids brood their eggs prior to hatching (e.g., *Nyctiphanes* spp.), whereas other species release eggs upon fertilization (e.g., *Euphausia pacifica* and *Thysanoessa spinifera*). Since adult euphausiids were not found in any stomachs in 1985 (Table 3), and since only the latter genera were encountered in large swarms in the study area in 1987 (Smith and Adams 1988), rockfish must have consumed eggs after release. It was not expected that a nonmotile prey would constitute such an important food resource to pelagic juvenile rockfish. The appearance of eggs in clumped masses in guts suggests that eggs were not individually picked from the plankton.

Another interesting finding was the consumption of fish larvae by bocaccio juveniles. A total 15–20% of all bocaccio sampled in 1984 and 1987 contained larval fish. In our surveys, bocaccio grow faster and reach larger sizes as pelagic juveniles ($\geq$100 mm SL) than do other species (Woodbury and Ralston 1991). They are also distributed at shallower depths (Lenarz et al. 1991).

We used the I_r statistic to rank the importance of individual prey items in the diet. This statistic differs from a similar statistic used by Hobson (1974) in that it is the product of proportional frequency of occurrence and percent by number, rather than percent by volume. Use of this statistic allowed us to characterize the prey types consumed by *Sebastes* in each of the 4 years studied. No obvious species-specific patterns emerged in the absence of a temporal component.

Our results indicate that pelagic juvenile *Sebastes* tend to respond similarly to environmental fluctuations in their food base, suggesting an opportunistic feeding strategy. Intraspecific dietary overlap between interannual pairings was much lower than were interspecific interannual pairings. On a relative basis, interannual differences in diet were tracked similarly among the five species we examined. Annual changes in diet are likely to reflect annual differences in the composition, availability, and abundance of prey.

It was not possible to infer from our results whether or not food is limiting to pelagic juvenile rockfishes, given the relatively large interannual variation in the diet among these species and the likelihood that variation in the availability of prey is likely responsible.

Even so, high dietary overlap observed among co-occurring pelagic juvenile rockfishes suggests that similar recruitment dynamics must exist if the distribution and abundance of foods has a major impact on recruitment.

Intraspecific spatial variation was observed (Table 7), even though substantial interspecific overlap exists in patterns of food utilization. In some instances, parallel spatial differences were observed for different species. For example, in 1987 both widow and shortbelly rockfish fed on euphausiid eggs to a much greater extent in deep water (>100 m) than in shallow water. In other cases, however, species-specific differences in diet due to depth were reversed. In 1987, for example, the consumption of *Calanus* spp. copepods by chilipepper was higher in shallow water, while consumption by widow rockfish was higher in deep water.

With the exception of the predator-size MANOVA discussed previously (i.e., shortbelly rockfish in 1985), sample sizes for each treatment combination in all MANOVA tests were reasonably well balanced. Therefore, it is unlikely that our conclusions were compromised by our choice of statistical tests.

The spatial incongruity of within-year dietary patterns among species also extended to interannual within-species comparisons. For example, shortbelly rockfish sampled in 1984 and 1987 consumed substantially fewer *Calanus* spp. copepods in the shallow southern quadrant than anywhere else. However, in 1986 consumption of this prey was greatest in fish taken in this region.

These interspecific (within-year) and interannual (within-species) comparisons demonstrate a lack of stability in the specifics of how spatial dietary effects are expressed. It is likely that the complex nearshore pattern of circulation that characterizes the study area (frontal structures, mesoscale eddies, turbulent jets, and upwelling plumes are common recurrent features; Mooers and Robinson 1984, Flament et al. 1985, Njoku et al. 1985, Schwing et al. 1990) defines the spatial distribution of the zooplanktonic animals upon which these rockfish feed. Thus, the dynamic nature of the physical environment off central California generates spatial instabilities in the distribution and abundance of prey.

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Age and growth of red hind *Epinephelus guttatus* in Puerto Rico and St. Thomas

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Abstract.—The red hind *Epinephelus guttatus*, a grouper of commercial importance in the central western Atlantic, is believed to be overexploited in a number of areas. Red hind taken by fish trap and hook-and-line in western Puerto Rico and the U.S. Virgin Island of St. Thomas were aged using sectioned otoliths (sagittae). Ages were validated by marginal increment analysis for fish ages 1–10 yr, and by a field study involving oxytetracycline injection for fish ages 1–4; a single opaque and translucent zone (viewed under transmitted light) is deposited annually. For Puerto Rico, the von Bertalanffy growth function (VBGF) was $L_t = 514.5\ (1 - e^{-0.101(t+2.94)})$. Back-calculated mean fork lengths ranged from 163 mm at age-1 yr, to 448 mm at maximum age-17. For St. Thomas, the VBGF was $L_t = 601.0\ (1 - e^{-0.071(t+4.69)})$. Back-calculated mean fork lengths ranged from 194 mm at age-1, to 470 mm at maximum age-18. Sex and stage of sexual maturation were determined for a subsample of aged fish from Puerto Rico. Fifty percent of females had attained sexual maturity by age 3 yr. Ages of females were 1–9 yr; males, 2–17 yr, and individuals undergoing sexual transition from female to male, 3–7 yr. The male to female sex ratio was 1:2.6. The occurrence of sexually-transitional individuals, as well as significant differences between the sexes in both size and age, confirm protogynous hermaphroditism for fish from Puerto Rico.

The red hind *Epinephelus guttatus* is a serranid of considerable commercial importance throughout the Caribbean, the Bahamas, and Bermuda (Burnett-Herkes 1975, Mahon 1987). In Puerto Rico and the U.S. Virgin Islands, this species is one of the most-frequently reported groupers in commercial landings. It is taken by hook-and-line, fish trap, and speargun, over the insular shelf to a depth of about 80 m.

Grouper are relatively long-lived and slow-growing fishes. These characteristics, combined with the protogynous sexual pattern (female to male sex change) reported for many grouper, and intensive fishing over short-term traditional spawning aggregations, render grouper species especially vulnerable to overexploitation (Bannerot et al. 1987, Manooch 1987, Ralston 1987, Shapiro 1987, Bohnsack 1989).

There are indications that red hind resources of Puerto Rico and the U.S. Virgin Islands are being overexploited. Commercial grouper landings reported in Puerto Rico have declined consistently and substantially over the last decade, from 386 mt in 1978 to 47 mt (of which 38% were red hind) in 1990 (Matos and Sadovy 1989, Sadovy In press, Sadovy and Figuerola 1992). Yield-per-recruit analyses indicate growth overfishing (harvesting at too small a size to maximize potential yield) in western Puerto Rico (Stevenson 1978, Sadovy and Figuerola 1992). All known annual spawning aggregations in both Puerto Rico and St. Thomas are heavily exploited. In addition, recent length-frequency data from commercial catches in St. Thomas indicate that mean length declined substantially between 1984 and 1988 (Beets and Friedlander 1992), although it is not clear to what extent this decline is attributable to overfishing, or is related to annual variation in recruitment (Appeldoorn et al. 1992), or a combination of the two.

Little is known of the life history of the red hind. Previous studies on age and growth in this species have been conducted in Bermuda using whole otoliths (Burnett-Herkes 1975), and in Jamaica using length-frequency analysis (Thompson and Munro 1974). However, neither study is recent and neither validated the ageing techniques. The sexual pattern is reported to be protogyny in Bermuda (Smith 1959, Burnett-Herkes 1975), and protogyny is also indicated for Puerto Rico stocks (Shapiro et al. unpubl. data). The objectives of this study were to determine age and growth of the red hind in two heavily-exploited areas—western Puerto Rico and St. Thomas, U.S. Virgin Islands—and to confirm sexual pattern. This information is necessary to allow stock assessments to be made for this species, and to permit the development of a management policy for the red hind in the region.

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Methods

Samples of *Epinephelus guttatus* were obtained from local fishermen and from Fisheries Research Laboratory (FRL) research programs using hook-and-line and arrowhead fish traps (3.2 cm (1.25 in.) galvanized mesh). Monthly collections were made between September 1987 and January 1989 with a minimum of 80 fish for most months from Puerto Rico. Smaller monthly samples from February 1988–January 1989 were received from St. Thomas, which lies on the same geological platform. Fish from St. Thomas were taken by hook-and-line and by fish trap (3.81 cm (1.5 in.) galvanized mesh).

For each fish, the weight (whole weight to nearest gm) and length (fork length (FL) and standard length (SL) to nearest mm) were measured. Otoliths (sagittae) were extracted, washed, and stored dry prior to processing. Preliminary work determined these calcareous structures to be more suitable than other calcareous structures for ageing purposes: dorsal spines exhibited growth lines but the central portion was often eroded resulting in an incomplete growth history, and scale markings were irregular and thus considered unreliable for ageing. Gonads in good condition were removed whenever possible, fixed in Davidson's fixative (Yevich and Barszcz 1981), embedded in paraffin, sectioned at 8 μm, and stained with hematoxylin and eosin.

Examination of whole otoliths under transmitted light revealed alternating opaque and translucent zones (terminology follows that of Wilson et al. 1983). To count the zones, however, otoliths had to be sectioned. Preliminary sectioning in two planes (frontal and transverse; $N = 20$ otoliths in each plane) established that transverse sections most clearly revealed growth zones. For sectioning, otoliths were mounted with glue, using a hot glue gun, on small cards, and sectioned through the focus with a single 7.2 cm (3 in.) diameter, low-concentration diamond blade on a Buehler Isomet low-speed saw. From each otolith, three sections of 0.36–0.43 mm were mounted on glass slides using Flo-Texx mounting medium.

Otolith width (OW) of a sample of unsectioned otoliths from a wide size-range of fish was measured to describe the OW/FL relationship. Measurements of otolith sections were made from the point where the sulcus meets the focus to the dorsal margin of the otolith (the region of most rapid growth) and to the proximal edge of each opaque zone. Measurements were also made from the distal edge of the outermost (opaque) zone to the dorsal margin for marginal increment analysis. Total number of opaque zones was noted. Measurements were made with an ocular micrometer, to the nearest micrometer unit (where 1 mm = 32 micrometer units). Each otolith was read twice. When readings disagreed by more than one opaque zone, the otolith was eliminated. Readings of a subsample of otoliths from Puerto Rico, of a wide range of ages and size-groups, were also made by an independent researcher.

To validate the temporal significance of opaque zones, a field study was undertaken. Individuals were captured by hook-and-line baited with squid from a 30 × 30 m area on a shallow (7 m) relatively-unfished reef known as "El Negro," 6 km off western Puerto Rico. The study site was visited over a 15-month period between April 1988 and June 1989. Individuals were tagged with a numbered FLOY anchor tag inserted into the dorsal musculature, and/or with FLOY abdominal tags for identification. Each fish was measured (FL) and injected with a dosage of 100 mg/kg body weight of Terramycin 100 (Pfizer) (1 mL contains 100 mg oxytetracycline-OTC-hydrochloride), and released. The dosage necessary to produce a visible mark under longwave ultraviolet light was established by preliminary tests (50 and 100 mg/kg body weight were tested; 50 mg/kg body weight did not consistently leave OTC marks) and the correct dosage determined on-site from a weight/FL relationship. Fish recaptured were measured and the otoliths examined for opaque zone formation following deposition of the OTC time marker.

Data were analyzed separately for Puerto Rico and St. Thomas using Lotus 1-2-3 and Basic Fishery Science Programs (Saila et al. 1988). The Kolmogorov-Smirnov two-sample test and the t-test were used to compare size-frequency distributions and mean size, respectively (Sokal and Rohlf 1981). Weight (W) on FL regressions were calculated using the relationship $W = aFL^b$. The SL:FL and OW:FL regressions were determined. The Lee method (Carlander 1981) of back-calculating body length from prior annuli was used:

$$L_i = a + [(L_c - a)(O_i/OR)],$$

where: L_i = length at time of ith annulus formation
a = intercept
L_c = length at time of capture (FL)
O_i = otolith radius at time of ith annulus formation
OR = otolith radius at time of capture.

This method requires knowledge of the relationship between OR along the line of measurement and FL. The constant a is obtained from this relationship and used in Lee's formula.

Growth was assumed to conform to the von Bertalanffy growth function (VBGF) (Ricker 1975). This

was calculated from the Saila et al. (1988) statistical package (FISHPARM program using Marquadt's non-linear least-squares method) and fitted to mean back-calculated lengths-at-age. The VBGF is

$$L_t = L_\infty (1 - e^{-K(t-t_0)}),$$

where L_t = length at age t
L_∞ = asymptote of the growth-in-length curve
K = Brody growth coefficient
t = age of the fish
t_0 = the theoretical origin of the growth curve, i.e., age at which fish would have zero length if it had always grown in a manner described by the equation.

To establish chronological age at the time of first opaque zone formation, data on the early growth of juvenile red hind were assembled from field collections and observations taken over 9-month periods following spawning in January of 1985 and 1987 (Sadovy, unpubl. data). Since spawning occurs over a limited period, during, at most, 2 months each year (Erdman 1976, Beets and Friedlander 1992, Shapiro et al. In press), and settlement may be assumed to occur between 3 weeks to 2 months after spawning (Colin et al. 1987), growth rates of individuals in the months following settlement could be estimated.

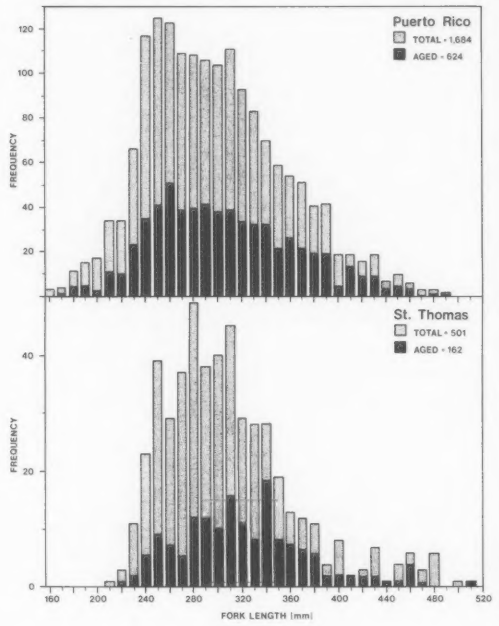

Figure 1
Size-frequency distributions of all *Epinephelus guttatus* collected (stippled) from Puerto Rico and St. Thomas, and subsamples from which otoliths were analyzed (solid).

Results

Samples

Of 1684 *Epinephelus guttatus* collected from Puerto Rico, otoliths were sectioned from 1098. Opaque and translucent zones were detectable in almost all otolith sections. When zones lacked sufficient definition for focus-to-ring measurements, the otoliths were discarded as unsuitable for use in calculating growth parameters, although some were used to assign ages to sexed fish by counts of opaque zones. A total of 624 (63%) otoliths were used to count growth zones and for focus-to-ring measurements. Of these, a subsample of 73 otoliths was read by an independent researcher; only one was rejected because of a discrepancy of more than one zone compared with our readings. Of the 501 St. Thomas samples, otoliths were sectioned from 490, and 162 (33%) were judged to be sufficiently clear for analysis; it is not known why otolith legibility was so low for St. Thomas samples.

Size-frequency distributions of all fish collected in Puerto Rico and in St. Thomas, and the subsamples used for analysis of otoliths from each location, are shown in Figure 1. For Puerto Rico, size-frequency distributions of individuals and subsamples used for age determination did not differ significantly (Kolmogorov-Smirnov: $D = 0.043$, NS). This confirmed our impression that illegible otoliths occurred at all fish sizes and ages, and affirmed that their elimination introduced no bias to the calculation of growth parameters. For St. Thomas, however, the distributions differed significantly ($D = 0.150$, $p < 0.05$). Therefore, growth parameters derived for St. Thomas should be treated with caution.

Frequency distributions of the distance from the focus to each opaque zone in Puerto Rico collections are shown in Figure 2. Relationships of SL:FL and W:FL were established for each location.

Puerto Rico:

$$FL = 3.86 + 1.2044\ SL \qquad (r^2\ 0.99;\ N\ 227)$$
$$\text{Log } W = -5.21 + 3.1422\ \text{Log FL} \qquad (r^2\ 0.97;\ N\ 1619)$$

St. Thomas:

$$FL = 24.49 + 1.1101\ SL \qquad (r^2\ 0.98;\ N\ 494)$$
$$\text{Log } W = -4.68 + 2.9402\ \text{Log FL} \qquad (r^2\ 0.92;\ N\ 493)$$

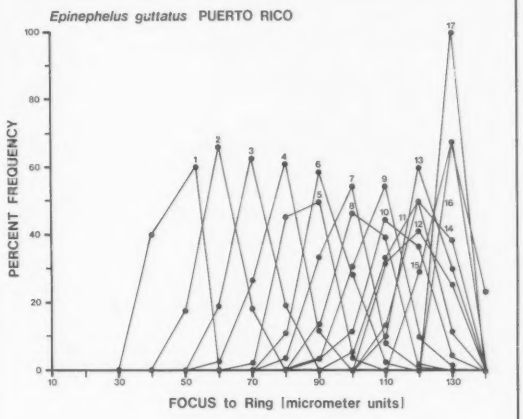

Figure 2
Frequency distributions of the distance from focus to proximal edge of each opaque zone (1–17) in sectioned sagittae of *Epinephelus guttatus* from Puerto Rico.

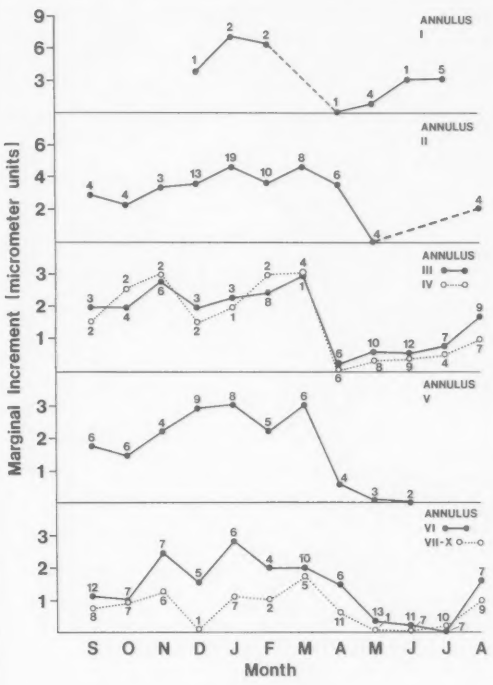

Figure 3
Marginal increment analyses for annuli I–X for *Epinephelus guttatus* from Puerto Rico (1 micrometer unit = 0.031 mm). Numbers above plots are sample sizes. Dashed lines connect samples separated by more than one month.

Validation

Marginal increment analysis Mean marginal increments for Puerto Rico fish were plotted on a monthly basis for annuli I–VI individually, and combined for annuli VII–X because of low monthly sample sizes for these older age-groups (Fig. 3). These data indicate that, at least for annuli II–V, the opaque zone begins to form between about April and May and is a true annulus. For annulus VI, the zone is laid down later, between May and July. For annuli VII–X combined, opaque zones are apparently deposited annually between May and July.

Since sample sizes from St. Thomas were too low for marginal increment analysis by individual age-group, otoliths from all age-groups were combined and plotted on a monthly basis by the percent of sections that lacked a marginal increment. These data indicate that the time of opaque zone formation (i.e., spring/summer) is similar for both Puerto Rico and St. Thomas (Fig. 4). A possible 'pseudoannulus' was detected in 74 (12%) of sectioned otoliths. This was a wide, weakly-discernible band always located between the focus and the first annulus. It occurred sporadically in fish of all sizes.

Field validation study Of a total of 139 fish tagged, injected, and released, 8 females from age-classes 1–4 were recaptured 5–16 months following tagging. Mean monthly growth rates for recaptured individuals from Puerto Rico measured 1–8 mm (Table 1). One individual (#00038) was recaptured in February 1991, 18 km from the tagging site on an offshore bank, a known spawn-

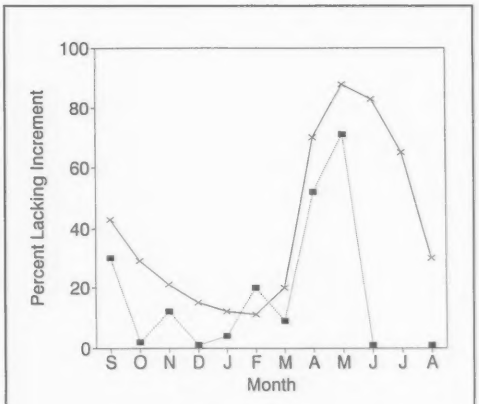

Figure 4
Percentage of otolith sections lacking a marginal increment for *Epinephelus guttatus* from Puerto Rico (solid line) and St. Thomas (dashed line) for age groups 1–10.

Table 1

Temporal significance of opaque growth zones in otoliths of *Epinephelus guttatus* from Puerto Rico, based on OTC-marked/recaptured fish. OR = otolith radius; MI = marginal increment; OTC = oxytetracycline mark.

Tag no.	Date (D/M/Y) Capture Recapture	FL (mm) Capture Recapture	Days in field	Measurements (32 micrometer units = 1 mm) Focus to ring 1	2	3	4	OTC	OR	MI	No. of opaque zones
00094	01/06/88 31/10/88	163 203	152	37*	—	—	—	[1]46	55	4	1
00078	25/05/88 04/05/89	127 151	344	45*	59	—	—	[1]52	63	0	2
00076	01/06/88 14/02/89	202 231	258	40	52	61	—	[2]65	72	4	3
00468	13/05/88 20/03/89	210 220	311	38	54	60	—	[2]68	73	5	3
00418	02/06/88 31/10/88	214 220	151	34	51	62*	—	[1]64	71	0	3
00385	19/08/88 10/02/89	218 248	175	39	50	69	—	[3]60	70	0	3
[4]00038	11/10/89 14/02/91	261 289	491	43	61	75	—	[3]72	85	3	3
00426	08/06/88 07/02/89	287 317	244	45	60	73	87	[2]90	95	4	4

[1]OTC mark lies within opaque zone indicated by asterisk.
[2]OTC mark lies at junction of opaque and translucent zones.
[3]OTC mark lies within translucent zone.
[4]Fish originally tagged June–December 1988; inner OTC mark 52[(3)]. Retagged 11/10/89 (only retag data presented).

Table 2

Mean back-calculated and observed fork lengths (mm) at time of opaque zone formation (yr) for age-groups 1–17 of 624 *Epinephelus guttatus* from Puerto Rico.

Age-group	*N*	Mean length at capture	SD	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	19	184	47	161																
2	97	247	21	168	213															
3	90	256	23	162	203	234														
4	52	272	26	159	195	226	253													
5	87	306	30	163	205	237	263	286												
6	126	321	33	165	207	237	262	283	303											
7	52	342	42	163	205	236	262	284	305	325										
8	29	353	34	169	209	236	260	283	304	320	336									
9	26	374	36	160	209	241	269	290	310	327	340	357								
10	27	393	32	170	213	244	271	293	312	329	346	361	374							
11	5	413	41	163	211	247	270	298	315	333	349	366	382	399						
12	4	416	30	160	194	226	257	283	302	321	335	352	366	382	394					
13	2	422	17	168	219	250	275	296	313	334	347	360	372	384	399	410				
14	5	448	31	172	212	247	278	304	323	340	354	368	383	409	417	432				
15	0	—	—																	
16	1	448	—	155	213	238	262	277	289	308	332	353	372	387	393	405	414	424	436	
17	2	458	46	159	216	247	271	293	312	323	336	348	362	380	395	406	416	431	440	448
Back-calculated mean lengths (weighted)				164	206	236	262	286	306	326	342	359	375	390	401	412	426	429	439	448
Growth increments					42	30	26	24	20	20	16	16	16	15	11	11	14	3	10	9

ing aggregation area. To reach the bank, this fish must have crossed water of at least 194 m depth, a substantial depth for similar-sized individuals of this species (Sadovy et al., unpubl. data).

During the tagging study, significant data loss occurred; in approximately 60% of tagged fish resighted, the identifying number of the dorsal tag had detached, leaving behind a monofilament anchor partially embedded in dorsal musculature. On the other hand, resightings of fish marked with abdominal tags indicated that all had retained both the numbered tag anchor and the attached color streamer.

Data for age-groups of recaptured fish indicated that no more than one opaque zone is deposited annually, although sample size was limited. Opaque zone formation had begun in or after February, had terminated prior to August, and occurred somewhat later in the year in older age-groups.

Recaptures were initiated as early as 5 months after tagging because individuals typically disappeared from the immediate study site within a few months of capture. Results covering less than a 12-month field period should be treated with caution, although all results were consistent with the marginal increment analysis in terms of both the temporal nature of opaque zones and the time of their annual deposition.

Age and growth

For Puerto Rico, the FL/OR relationship is

$$FL = 33.2180 + 3.0743\ OR \quad (r^2\ 0.76;\ N\ 624).$$

Table 2 shows the mean back-calculated lengths for ages 1–17 years from 624 fish. The following growth parameter estimates were obtained from the von Bertalanffy growth function (with asymptotic SE in parentheses):

$$L_\infty = 514.5\,\text{mm FL} \quad (6.29)$$
$$K = 0.1013 \quad (0.003765)$$
$$t_0 = -2.944 \quad (0.1357).$$

Figure 5 shows empirical mean lengths and their standard deviations, as well as back-calculated and theoretical (VBGF) growth curves, for Puerto Rico.

For St. Thomas the FL/OR relationship is

$$FL = 94.7206 + 2.4757\ OR \quad (r^2\ 0.68;\ N\ 162).$$

Table 3 shows the mean back-calculated lengths for age-groups 1–18 from 162 fish. The following growth parameter estimates were obtained from the von Bertalanffy growth function (with asymptotic SE in parentheses):

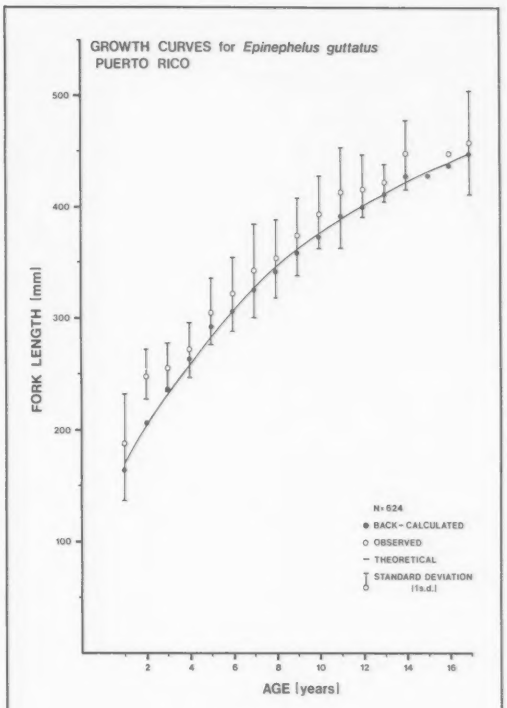

Figure 5
Empirical, back-calculated, and theoretical (von Bertalanffy) growth curves for *Epinephelus guttatus* from Puerto Rico.

$$L_\infty = 601.0\,\text{mm FL} \quad (32.82)$$
$$K = 0.0705 \quad (0.009954)$$
$$t_0 = -4.690 \quad (0.5920).$$

Figure 6 shows the empirical mean lengths and their standard deviations, as well as back-calculated and theoretical growth curves, for St. Thomas.

For Puerto Rico, the OW/FL relationship is

$$OW = 1.4205 + 0.0108\ FL \quad (r^2\ 0.93;\ N\ 315;\ \text{Fig. 7}).$$

For St. Thomas, the OW/FL relationship is

$$OW = 0.5591 + 0.0049\ FL \quad (r^2\ 0.93;\ N\ 101).$$

When mean back-calculated fork lengths for annuli I–V for age-groups 1–14 from Puerto Rico and St. Thomas are plotted (Fig. 8), two points are worthy of note. If regressions for each annulus are calculated for all available ages up to age-group 14, all are statistically

Table 3

Mean back-calculated and observed fork lengths (mm) at time of opaque zone formation (yr) for age-groups 1–18 of 162 *Epinephelus guttatus* from St. Thomas.

Age-group	*N*	Mean length at capture	SD	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	7	249	12	204																	
2	10	260	17	195	232																
3	39	280	25	190	229	259															
4	10	284	28	185	213	243	265														
5	16	319	28	195	229	260	286	308													
6	27	335	27	195	228	255	278	298	316												
7	11	348	29	194	227	255	278	297	317	333											
8	13	362	29	195	230	258	282	303	320	333	349										
9	9	370	55	195	226	252	275	296	315	331	343	358									
10	5	356	28	184	212	238	261	279	296	312	324	333	345								
11	5	391	45	195	228	253	279	300	317	332	345	355	367	378							
12	3	424	51	203	242	273	294	311	329	346	358	375	388	401	411						
13	1	460	—	206	234	270	290	332	348	365	382	396	410	424	438	452					
14	3	442	22	222	246	269	291	318	339	355	368	378	391	399	412	420	430				
15	2	492	12	215	263	290	316	343	362	378	389	405	421	434	450	460	469	478			
16	0	—	—																		
17	0	—	—																		
18	1	475	—	192	217	248	273	299	324	350	368	386	401	414	427	432	439	452	460	465	470
Back-calculated mean lengths (weighted)				194	228	256	279	301	318	335	349	362	377	400	423	438	445	469	460	465	470
Growth increments					34	28	23	22	17	17	14	13	15	23	23	38	7	24	−9	5	5

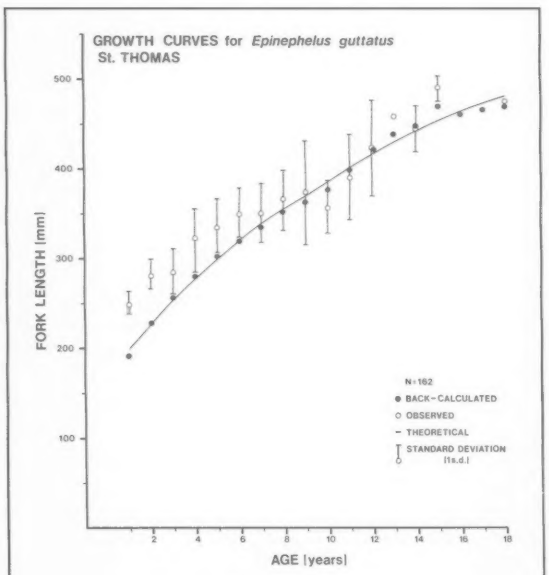

Figure 6

Empirical, back-calculated, and theoretical (von Bertalanffy) growth curves for *Epinephelus guttatus* from St. Thomas.

significant ($p<0.05$), with the exception of annuli I and II for Puerto Rico. Also of note are two distinct depressions in back-calculated mean lengths for each geographic location. For Puerto Rico these are indicated at age-groups 4 and 12, and for St. Thomas at age-groups 4 and 10. These points will be addressed in the discussion.

Data on growth during the months following spawning indicate rapid growth from the time of settlement in February or March at ~40 mm FL (*N* 29), to 60 mm FL in April/May (*N* 3), 108 mm (*N* 2) in August, and 115 mm (*N* 4) in October.

Age, sex, and size

A total of 186 individuals from Puerto Rico were sexed, by histological examination of gonads, and aged. Of these, 131 were female and 50 were male; 5 were considered to be in sexual transition between female and male, with gonads consisting of degenerating sexually-mature (i.e., vitellogenic) ovarian tissue and scattered areas of spermatogenic tissue exhibiting various stages of spermatogenesis (Sadovy and Shapiro 1987). All males exhibited testes with an ovarian-like configuration and lumen (Sadovy and Shapiro 1987).

Mean observed FL, standard deviation, and sample size by sex and age-class from Puerto Rico are shown

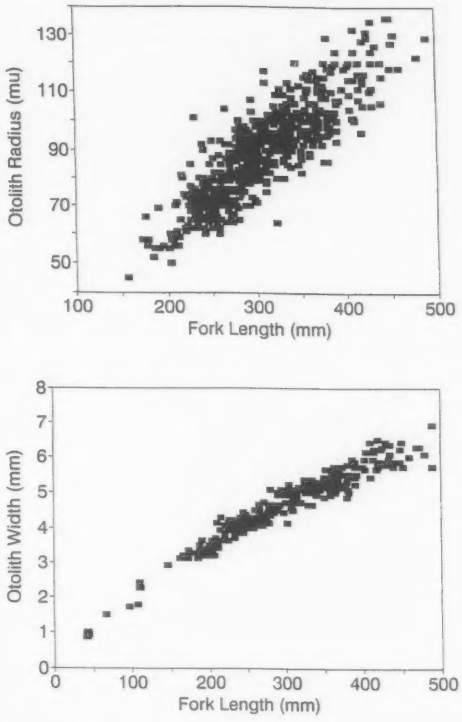

Figure 7

(upper) Relationship between otolith radius and fork length for *Epinephelus guttatus* from Puerto Rico (1 micrometer unit = 0.0312 mm). (lower) Relationship between unsectioned otolith width and fork length for *Epinephelus guttatus* from Puerto Rico.

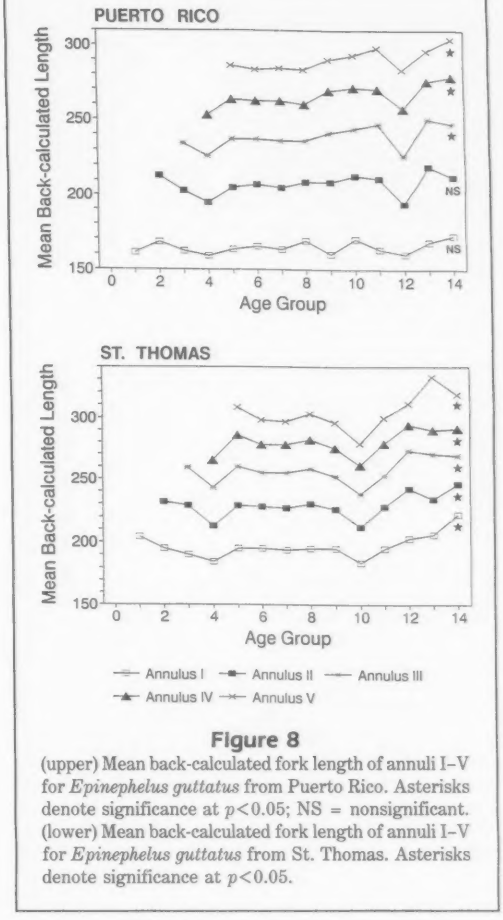

Figure 8

(upper) Mean back-calculated fork length of annuli I–V for *Epinephelus guttatus* from Puerto Rico. Asterisks denote significance at $p<0.05$; NS = nonsignificant. (lower) Mean back-calculated fork length of annuli I–V for *Epinephelus guttatus* from St. Thomas. Asterisks denote significance at $p<0.05$.

in Table 4. Fork length at time of capture (i.e., observed FL) did not differ significantly between the sexes for age-groups 2–8 (Table 4). However, both age- and size-frequency distributions from both Puerto Rico and St. Thomas differed significantly by sex (age: $D=0.593$, $p<0.01$; size: $D=0.576$, $p<0.01$) (Fig. 9).

Females were found at ages 1–9, males at ages 2–17, and individuals undergoing sexual transition at ages 3–7 (Table 4). No sexually-mature individuals were detected below age 2 years. Fifty percent of females had attained sexual maturity by age 3.

Discussion

Validation and formation of opaque zones

Opaque zones incrementally deposited in the sagittae of the red hind *Epinephelus guttatus* were validated as annual in this study, both by marginal increment analysis and by a field study involving the marking of otoliths by OTC. Although the possibility of bi- or multi-annual growth lines (Deelder 1981, Lee et al. 1983) for fish aged 11 years and over could not be discarded, these age-groups constituted a small percentage of sampled individuals; hence, the validation may be applied confidently to the exploited segment of red hind stocks in the region.

It is not known what causes the formation of opaque and translucent zones in this species. However, since zones are found in both adults and juveniles, they are clearly not caused exclusively by spawning activity (Nekrasov 1980). Opaque zone formation has been proposed to be associated with low somatic growth rates, and translucent zones with high growth rates, in the white grunt *Haemulon plumieri* (Sadovy and Severin 1992). A similar relationship is proposed for the red

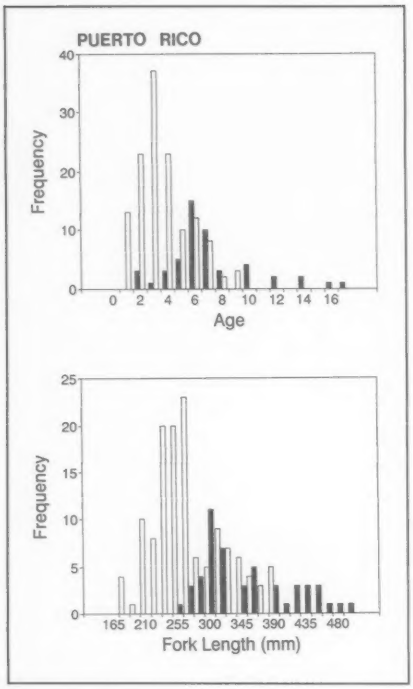

Figure 9
(upper) Age-frequency distributions of female (stippled) and male (solid) *Epinephelus guttatus* from Puerto Rico. (lower) Size-frequency distributions of female (dotted) and male (solid) *Epinephelus guttatus* from Puerto Rico.

hind (Sadovy and Severin, unpubl. data). Since time of opaque zone formation was earlier in the year in younger than in older fish, zone formation is unlikely to be caused by a simple environmental factor acting directly and equally on all individuals. Time of opaque zone formation is February–July, which is similar to that reported for four other groupers of the genus *Epinephelus* from the western Atlantic (Table 5). The pattern of earlier annual opaque zone formation in younger individuals noted in our study was also reported in otoliths from *E. morio* (Moe 1969) and *Mycteroperca microlepis* (Collins et al. 1987), and in pike *Esox lucius* (aged using cleithra; Casselman 1983).

Data on growth of red hind in the months following settlement indicate rapid growth from the time of settlement at ~40 mm FL (N 29), to 115 mm FL the following October. These data indicate that the first opaque zone, which is laid down between March and April at a back-calculated 164 mm FL (SD 18 mm) in Puerto Rico and 194 mm FL (SD 17 mm) in St. Thomas, represents an age 1+ year fish (13–15 months old, depending on month of spawning).

Growth parameters and longevity

Red hind in Puerto Rico and St. Thomas are long-lived and attain their maximum size slowly, following fast growth during the first year. Thompson and Munro (1974), using length-frequency analysis, calculated L_∞ = 520 mm FL for Jamaica–Pedro Bank fish, and L_∞ = 500 mm FL for Jamaica-Port Royal fish. Burnett-Herkes (1975),

Table 4
Mean observed fork length (mm) and standard deviation for male and female red hind, *Epinephelus guttatus*, by age-group. Fish from Puerto Rico collected September 1987–September 1988 (*$p<0.05$). NS = nonsignificant.

	Observed fork length (mm)								
	Female			Male			Student's	Transitional fish	
Age	$\bar{x}$	SD	N	$\bar{x}$	SD	N	t	FL	N
1	196.3	16.3	13	—	—	—	—		0
2	238.7	20.6	23	253.7	34.2	3	1.1076 NS		0
3	251.5	18.6	37	301.0	—	1	0.1410 NS	275	1
4	267.2	28.0	23	280.7	10.5	3	0.8150 NS	278	1
5	307.2	28.4	10	288.0	7.3	5	1.4621 NS		0
6	344.9	35.8	12	322.2	30.4	15	1.7823 NS	315	1
7	340.6	25.9	8	336.6	49.4	10	0.2066 NS	258; 380	2
8	362.5	17.5	2	368.7	50.4	3	0.2536 NS		0
9	326.7	12.5	3	—	—	0	—		0
10	—	—	—	418.0	14.9	4	—		0
11	—	—	—	—	—	0	—		0
12	—	—	—	440.0	10.0	2	—		0
13	—	—	—	—	—	0	—		0
14	—	—	—	470.0	10.0	2	—		0
15	—	—	—	—	—	0	—		0
16	—	—	—	448.0	—	1	—		0
17	—	—	—	490.0	—	1	—		0
Total	268.0	50.0	131	342.0	65.0	50	8.1597*	301	5

Table 5
Caribbean and western Atlantic *Epinephelus* spp. aged by whole or sectioned otoliths.

Species	Growth parameters* L_∞ (mm FL)	K	t_0 (yr)	Time of opaque zone formation	Max. age (yr)	Source
E. nigritus	2394	0.054	−3.616	April–May	41	Manooch and Mason 1987
E. niveatus	1320	0.087	−1.012	May–July	17	Moore and Labisky 1984
E. niveatus	1255	0.074	−1.920	May–July	17	Matheson and Huntsman 1984
E. drummondhayi	967	0.130	−1.010	April–June	15	Matheson and Huntsman 1984
E. morio	928	0.113	0.091	—	14+	Melo 1975 (cited in Manooch 1987)
E. morio	792	0.179	−0.449	March–July	25+	Moe 1969
E. guttatus	601	0.071	−4.690	March–June?	18+	This study; St. Thomas
E. guttatus	515	0.101	−2.944	February–July	17+	This study; Puerto Rico
E. guttatus	507	0.180	−0.440	—	17+	Burnett-Herkes 1975; also used length-frequency data

*L_∞ = asymptote of the growth-in-length curve; K = Brody growth coefficient; t_0 = theoretical origin of von Bertalanffy growth curve (Ricker 1975).

using whole otoliths and length-frequency analyses for ageing, reported L_∞ = 507 mm FL in Bermuda. The largest fish sampled in the present study were 490 mm FL in Puerto Rico and 504 mm FL in St. Thomas. In several years of intensive sampling of thousands of red hind from local commercial landings, Fisheries Research Laboratory (FRL) data recorded <2% of individuals >500 mm FL (FRL, unpubl. data). These data reflect asymptotic lengths established in the present study. Randall (1983) reported the largest West Indian specimen collected to be 673 mm FL, and Smith (1971) reported the largest fish he examined to be 510 mm SL (618 mm FL using the above FL/SL relationship).

Growth parameters obtained using otoliths as the ageing structure for western Atlantic species of the genus *Epinephelus* are shown in Table 5. The data for *E. guttatus* in Puerto Rico and St. Thomas fall within the range of values of L_∞, K, and maximum age reported for western Atlantic grouper. A maximum of 17 growth zones in Puerto Rico and 18 growth zones in St. Thomas were recorded. We consider the estimated longevity of 17+ and 18+ to be reasonable for commercially-taken red hind in Puerto Rico and St. Thomas, respectively. Luckhurst et al. (1992) recorded 22 (±1) opaque zones in an unusually-large 720 mm FL individual from Bermuda.

Lengths-at-capture were consistently higher than back-calculated lengths for each age-group (Figs. 5, 6). The higher observed mean fork lengths generally reflect additional growth between previous ring formation and time of capture. However, the notably high observed mean FL of ages-1 and -2 fish for both Puerto Rico and St. Thomas may be due, in part, to selection by the fishery of the largest fish in these younger age-groups. Similar selection was also reported for the first two age-classes in *E. morio* (Moe 1969) and may be especially common in longer-lived, slower-growing species, such as grouper (Bannerot 1984). When sampling is biased towards larger individuals of young year-classes, there may be artificial depression of K in the VBGF (Ricker 1975). A downward bias would generally produce conservative management advice in terms of justifying imposition of minimum size regulations based on future returns to the fishery (Bannerot 1984).

The relationship between FL and OR for both locations is somewhat weaker than in other studies of fish age and growth. Since the OW/FL relationships for otoliths from both locations are strong, this indicates that variability is introduced by the position on the sectioned otolith selected for measurement and counting of opaque zones, rather than by a poor relationship between body length and otolith size (Fig. 7).

The regressions for mean back-calculated fork lengths of annuli I–V of age-groups 1–14 for Puerto Rico and St. Thomas are statistically significant, with two exceptions (Fig. 8). Such a trend could suggest a reverse "Rosa-Lee" phenomenon, indicating enhanced survivorship of fast-growing fish (Ricker 1975). If this were true, it would result in an upward bias of the parameter K in the VBGF. However, sample sizes for individuals above age-group 10 are very low, and regressions for age-groups 5–10 are not significant, with the exception of annulus II for Puerto Rico. Since these age-groups comprise the bulk of commercial landings, we believe that bias to estimates of growth parameters derived in the present study is negligible. Furthermore, since a similar increase is apparent in most age-groups

below age-group 4, there is clearly no consistent relationship between growth rate and mortality.

The depressions in back-calculated mean lengths (Fig. 8) apply to years 1983–84 (age-group 4) and 1975–76 (age-group 12) for Puerto Rico, and 1984 (age-group 4) and 1978 (age-group 10) for St. Thomas. In the case of older age-classes, small sample sizes could have produced sampling errors. However, we believe that in the case of 1984, this pattern is unlikely to be the result of sampling artifacts. Possible explanations for lower mean back-calculated lengths in both locations include environmental factors, such as unusually low temperatures or reduced food availability, or alterations in fishing effort and associated demographic changes. We know of no changes in fishing effort or gear during the early 1980s at either location. Reduced environmental temperatures or food availability may have caused age-1 and -2 fish to experience a decrease in growth rate that carried over into later years. Interestingly, catch curves developed from the same data set indicate a particularly low recruitment into the fishery of age-4 fish in 1984 (Sadovy and Figuerola 1992). This trend in the catch curves is strikingly similar for both locations, strongly suggesting a region-wide phenomenon. Poor recruitment into the fishery of a young age-class could result from slow growth early in life of individuals of that cohort.

Examination of temperature records for the region indicates that the winter of 1984 was the first since that of 1975 in which the mean minimum temperature dropped below 26°C (lat. 14.7°–18.2°) (Atwood and Hendee In press). In summary, we suggest that lower temperatures may have retarded growth in young individuals and that this reduction in size-at-age early in life was carried through the growth history of the animal.

Age and sex

Among sexed individuals, the majority (80%) of females were ages 1–5, and the males ages 2–10. Empirical mean lengths for age-groups 2–8 did not differ by sex. Moe (1969) also found the empirical growth curves of the sexes of *E. morio* to be similar, indicating that there are no marked differences in growth between the sexes or sexual phases of an individual. The combination of histological data, especially the presence of transitionals, size/age frequency distributions, and a female-biased sex ratio, confirm protogyny for this species in Puerto Rico. However, the presence of males as young as the youngest mature female indicates that at least some males may develop directly from a juvenile phase without passing through an initial functional female phase.

The red hind and fishery management

The condition of growth overfishing in the red hind (Sadovy and Figuerola 1992), and the general vulnerability of grouper species to fishing pressure, indicate the urgent need for management, stock monitoring, and assessment throughout its geographic range. In particular, given the apparent importance of spawning aggregations for annual reproductive output in the red hind (Bohnsack 1989; Shapiro 1987), and the intensity with which these are exploited locally (Sadovy, unpubl.), the possibility of recruitment overfishing needs to be addressed.

Acknowledgments

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Abstract.– Spawning patterns, larval distribution, and juvenile growth characteristics were examined for tautog *Tautoga onitis* in New Jersey and the Mid-Atlantic Bight. We analyzed data from plankton surveys (1972–1990) over the continental shelf and in the Great Bay–Mullica River estuarine system. Data on size and abundance of juveniles were derived from throw trap and trawl collections in New Jersey estuaries (1988–89). In addition, we validated the daily deposition of otolith increments and used increment counts to estimate juvenile age and growth patterns. Extensive egg and larval collections indicated that spawning occurs from April through September, with a peak in June and July. Spawning over the continental shelf is concentrated off Long Island and Rhode Island. Based on validated daily increments in sagittal otoliths and the formation of a well-defined settlement mark, tautog larvae spend about 3 weeks in the plankton. Both spawning and settlement occur over a prolonged period, based on otolith back-calculations. Three methods of estimating young-of-the-year growth rates, including length-frequency progressions, otolith age/fish-size comparisons, and direct measurement of growth in caging experiments, indicated an average growth rate of about 0.5 mm/day during the peak midsummer growing season. Length-frequency distributions suggested tautog reach a modal size of about 75 mm SL after their first summer, and 155 mm by the end of their second summer.

Early life history of the tautog *Tautoga onitis* in the Mid-Atlantic Bight*

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The tautog *Tautoga onitis* is one of two labrid wrasses common along the northeast coast of the United States (the other is the cunner *Tautogolabrus adspersus*). Tautog occur in coastal areas from Nova Scotia to South Carolina, but are abundant only from Cape Cod to the Delaware Capes (Bigelow and Schroeder 1953). Adult tautog form a minor component of local commercial fisheries and a major component of the recreational catch. They reach a maximum size of about 90 cm and 10 kg (Bigelow and Schroeder 1953), and an age of 34 years (Cooper 1967). Large juveniles and adults depend on young mussels *Mytilus edulis* for food (Olla et al. 1974), and the diet of recently-settled juveniles consists primarily of copepods and amphipods (Grover 1982). Spawning takes place from May to August, with a peak in June (Kuntz and Radcliffe 1918, Colton et al. 1979, Eklund and Targett 1990). Egg and larval development are described in detail by Kuntz and Radcliffe (1918) and Williams (1967); additional information on life history is presented in Auster (1989).

Both juvenile and adult tautog are dependent on habitats with structure or cover, which presumably aids in protection from predators (Olla et al. 1974 and 1979, Olla and Studholme 1975). Tautogs typically become quiescent at night, resting in association with some type of shelter (Olla et al. 1974). Smaller fish (subadults <25 cm) may range only a few meters from that shelter during daytime activity, while larger individuals (adults >30 cm) cover a broader area for foraging, returning to the same general shelter area at night (Olla et al. 1974).

Declining water temperatures in the fall trigger an offshore migration of adults (age 4+). An increase in schooling behavior and night activity also occurs (Olla et al. 1980), perhaps related to migratory activity. Laboratory studies indicate that adults attain a dormant state at temperatures <5°C. Juveniles (age 2–3) also become torpid in winter, but they remain inshore, either partially buried or in close proximity to structure (Olla et al. 1974). In spring and summer adults return to inshore habitats. On hard-bottom reefs off Maryland

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Table 1

Collection sources for *Tautoga onitis* eggs, larvae, and juveniles used in analyses of seasonal distribution and growth comparisons.

Stage	Sampling location	Years sampled	Sampling frequency	No. of tows or samples	Data source
Eggs	Mullica River, Great Bay, Little Egg Inlet	1972–75	monthly or bimonthly	462	Milstein and Thomas 1977
Larvae	Nova Scotia to North Carolina	1977–87	monthly or bimonthly	11,438	MARMAP
	Great Bay, Little Sheepshead Creek	1989–90	weekly	913	Rutgers Marine Field Station Plankton Survey
Early juveniles	Great Bay, Little Egg Harbor	1988–89	biweekly, May–September	436	Sogard and Able 1991
	Great Bay; artificial seagrass	1988	weekly, June–September	54	Sogard 1990
Late juveniles	Great Bay, Little Egg Harbor	1988–89	monthly	808	Rutgers Marine Field Station Trawl Survey

and Virginia (25–35 m in depth) fish-trap catches of tautog are lowest in summer (Eklund and Targett 1991), perhaps due to inshore migrations of winter residents. Tagging studies conducted by Cooper (1966) suggest relatively discrete populations of tautog, with adults returning to the same spawning location following their winter residence offshore.

These prior studies of habitat requirements, behavior, and growth have focused primarily on fishes older than 1 year. In this paper we concentrate on life-history aspects for young-of-the-year individuals, particularly larvae and juveniles that have just recently metamorphosed and settled from the plankton. We present information on spatial and temporal distribution of eggs and larvae, larval stage duration, juvenile habitat, daily growth, and otolith-size/fish-size relationships.

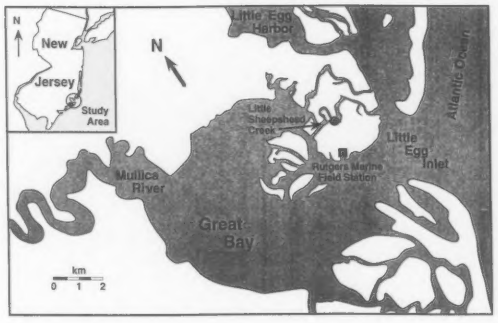

Figure 1

Map of Mullica River–Great Bay estuary system in New Jersey, and location of plankton sampling site in Little Sheepshead Creek.

Materials and methods

Reproductive seasonality and larval distribution

Information on timing of spawning and spatial distribution of tautog larvae was obtained from three sources (Table 1). Egg abundances were assessed in plankton collections during December 1972–December 1975 in the Mullica River–Great Bay estuary and adjacent ocean off Little Egg Inlet, New Jersey (Fig. 1). Sampling was conducted with 0.5 m and 1.0 m diameter plankton nets and 20 cm and 36 cm diameter bongo samplers with 0.5 mm mesh. Surface, midwater, and bottom tows were made with the plankton nets; the bongos were fished obliquely. Data used in this study were reanalyzed from a report by Milstein and Thomas (1977).

Larval occurrences over the continental shelf were determined from collections made on Marine Resources Monitoring, Assessment and Prediction (MARMAP) surveys (Sherman 1988) by the National Marine Fisheries Service (NMFS). Surveys were conducted from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia. Sampling stations are shown in Figure 2; sampling methods are described in Sibunka and Silverman (1989).

Our third source of plankton data was obtained from a sampling program at the Rutgers University Marine Field Station. A 1 m diameter, 1 mm mesh net was fished at the surface and just above the bottom on night flood tides in Little Sheepshead Creek, adjacent to Great Bay (Fig. 1).

Juvenile length-frequency comparisons

Monthly patterns in length-frequency distributions were assessed from collections across several sites in the Little Egg Harbor and Great Bay estuaries (Fig. 1) using throw-trap and otter trawl sampling (Table 1). A throw trap is a 1 m^2 open box that is thrown onto

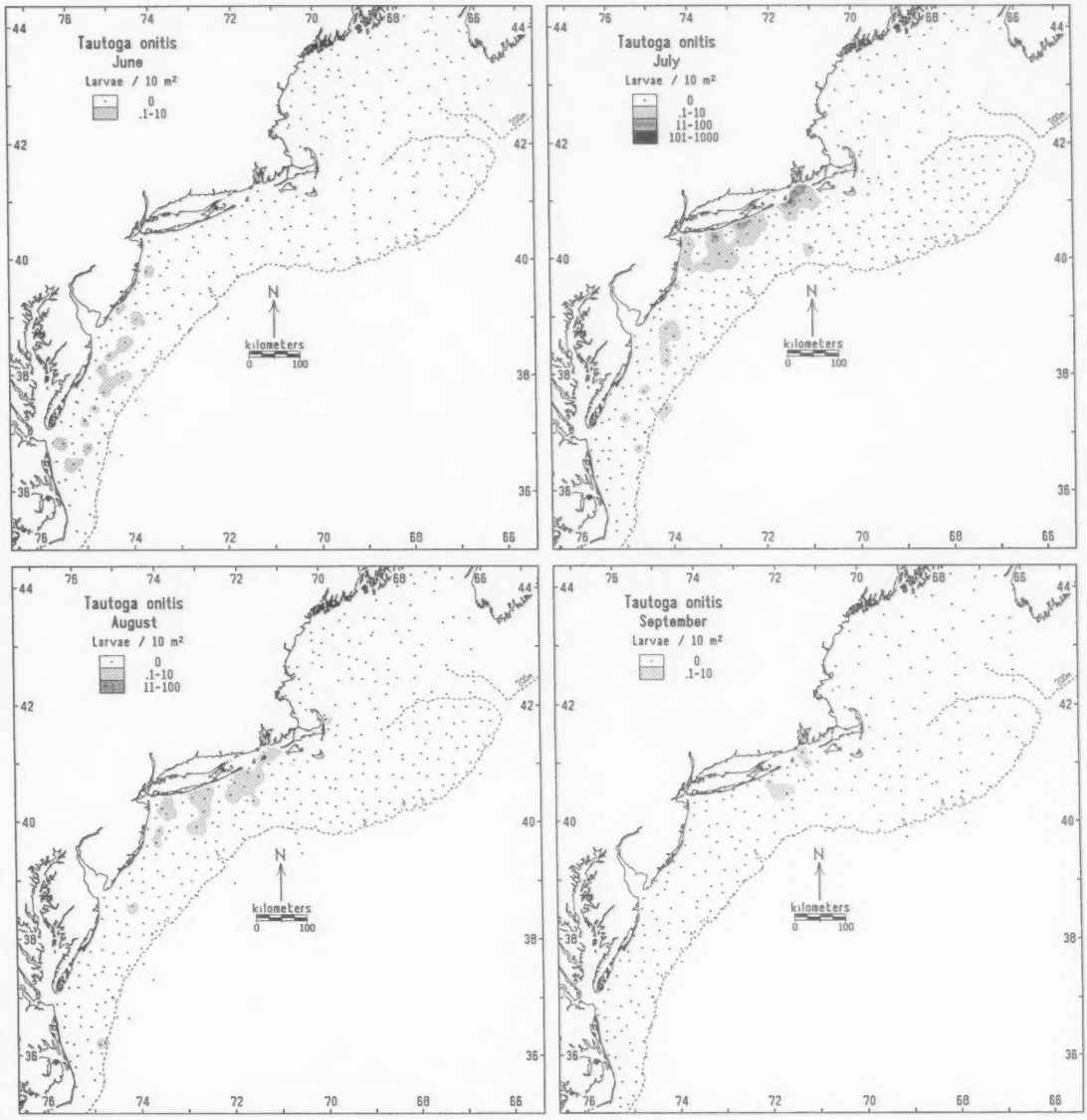

Figure 2

Average monthly distributions of *Tautoga onitis* larvae based on 11 years (1977–87) of sampling in the Mid-Atlantic Bight. Density calculations are based on collections within 1 km² blocks.

the desired substrate, with all animals subsequently removed with a 1 m wide net scraped across the bottom substrate. All throw-trap sampling was conducted at low tide in shallow (<0.5 m at low tide) vegetated and unvegetated habitats. Further details on the throw-trap method and sampling schedule are presented in Sogard and Able (1991). Additional length data were obtained from tautog collected with throw traps from artificial seagrass habitats on a shallow sandflat in Great Bay (Sogard 1990).

Tautog in deeper waters (1–8 m) of the Great Bay–Little Egg Harbor estuarine system were collected

during the Rutgers Marine Field Station trawl survey. A 4.9 m otter trawl (6.3 mm mesh cod end, 19 mm mesh wings) was towed for 2 minutes at a total of 14 stations, which were representative of a variety of habitat types. Four replicate trawls were taken at each station.

Otolith increment analysis

More detailed information on planktonic stage duration, settlement patterns, and growth of young-of-the-year tautog was derived from analysis of otolith increments. To validate a daily rate of increment formation, the number of increments following a tetracycline-induced fluorescent mark on the sagitta was compared with the actual number of days elapsed. Juvenile tautog (19–63 mm SL) were immersed for 24 h in a 500 mg/L solution of oxytetracycline dihydrate in natural seawater (20–25 ppt) diluted with distilled water to about 17 ppt. They were then held in laboratory aquaria, fed daily with *Artemia*, and preserved in 95% ethanol after 6–30 days. The sagittae of these individuals were removed, embedded in Spurr resin, and polished in the sagittal plane to the central primordium on both sides, using a series of 400–1500 grit sandpaper and alumina powder (0.3 μm), following the methods of Secor et al. (1991). The number of increments following the tetracycline mark was counted with UV microscopy at 400–1000× magnification.

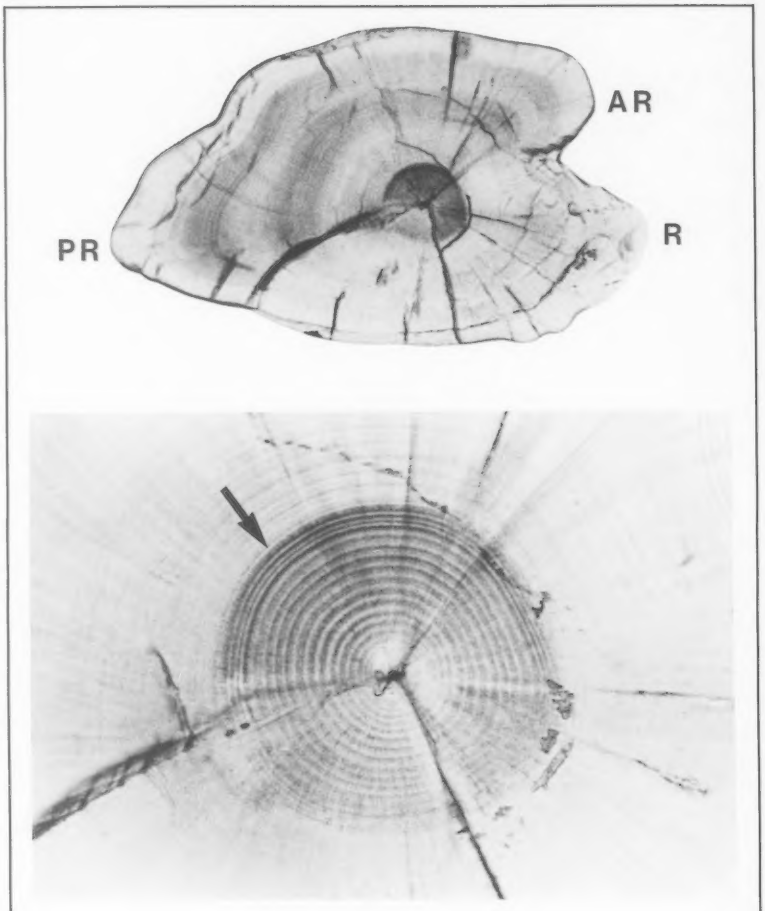

Figure 3
Ground and polished left sagitta of a 38.7 mm SL juvenile *Tautoga onitis*. (upper) Photographed at 100× magnification; scale bar = 200 μm. R = rostrum, PR = postrostrum, AR = antirostrum. Tip of the rostrum was partially destroyed during polishing. (lower) Closeup view of central region (400×). Arrow points to transition between pelagic and demersal stage increments. Scale bar = 50 μm.

The degree of correspondence between otolith size and fish size was determined for 55 juvenile tautog by comparing radial measurements of the rostrum, postrostrum, and antirostrum (Fig. 3) with standard lengths. Radial measurements were made with an image analysis system attached to an Olympus BH-2 microscope, using a magnification on the monitor of 160× or 410×, depending on the size of the otolith. The relationship between otolith radial measurements and length (SL) of the fish was determined by regression analysis. Because preliminary analysis of a matched set of sagittae found no significant differences between left and right radius measurements (paired comparisons t-tests: n 8, $P>0.10$ for all three radii), either sagitta was used in subsequent analyses.

Increments were counted for a series of tautog (n 37, 7.6–62.8 mm SL) collected from early-July through late-September in 1988. Larval and juvenile increments were distinguished on the basis of an apparent settlement mark in the sagittae (see below). Increments were counted independently on three different dates by the same reader, and the results were averaged. Preliminary counts of matched sagittae found no difference

between left and right (paired comparisons t-test: $P>0.10$), with the two sides differing by <2%. Thus, either sagitta could be used for increment counts.

The mean duration of the planktonic stage was estimated by the mean number of increments preceding the settlement mark. Birth and settlement dates were estimated by subtracting the number of total increments and juvenile increments, respectively, from the date of capture. Assuming that initial increment formation occurred at about the time of hatching, as in other wrasses (Victor 1982), our estimates of birthdates should correspond within a few days to the date of hatching.

Juvenile growth rates

We used three independent methods to estimate growth rates of young-of-the-year juveniles during the summer. The relationship between otolith age (total increments) and standard length was fit to a linear equation, using the slope as an estimate of daily growth. We also examined the progression of mean lengths for tautog collected on a weekly basis in 1988 (primarily from artificial seagrass experiments). Weekly mean lengths were determined and regressed on time, with the slope of the resulting equation used as a second estimate of daily growth. Growth rates based on these two indirect estimates were compared with a third, direct measurement of individual tautog growth in field caging experiments by Sogard (In press).

Results

Reproductive seasonality and larval distribution

In the Great Bay–Mullica River estuarine system, tautog eggs occurred in plankton collections from April through August, with peak abundances in June and July (Table 2). Initial occurrence and peak abundance of eggs were earlier in the Mullica River than in the bay and adjacent inlet, suggesting that spawning began earlier in the season in the upper part of the estuary, and continued later in the summer in the lower estuary and offshore waters. Tautog larvae in weekly plankton collections in Great Bay (Table 1) occurred in July and August of 1989 (n 12) and July of 1990 (n 9). Larvae were collected in the offshore MARMAP surveys from May through October, with a peak in July (Table 3, Fig. 2).

Based on geographic distribution of larvae, spawning was concentrated in southern New England waters (Fig. 2). Spawning activity in continental shelf waters appeared to follow a northward progression through the summer, beginning as early as May in the southern part of the region (Table 3).

Daily increment validation

Results of the validation tests indicated that increments on sagittae of juvenile tautog were deposited on a daily basis. The slope of the regression comparing the actual number of days elapsed with the number of increments following tetracycline marks did not differ from 1 ($P>0.05$, r^2 0.86, Fig. 4). Comparison of sagittal

Table 2

Monthly mean densities (no./1000 m³) of *Tautoga onitis* eggs in Mullica River, Great Bay, and adjacent Atlantic Ocean off Little Egg Inlet, New Jersey, December 1972–December 1975. Plankton sampling was conducted throughout the year, but eggs were not collected in months not appearing in the table.

	Mullica River	Great Bay	Atlantic Ocean
April	66	3	0
May	116	726	853
June	169	165	1259
July	22	2221	1984
August	0	13	20

Table 3

Abundance of *Tautoga onitis* larvae ($\bar{x}$ no./100 m³) collected during MARMAP survey cruises, 1977–87, by subarea and month. Mean abundance is followed by number of occurrences (2d line) and total number of stations sampled (3d line).

Subarea	May	June	July	Aug	Sept	Oct
Georges Bank	—	0.01	—	—	—	—
	0	1	0	0	0	0
	332	152	213	312	144	396
Southern New England	—	—	1.75	0.19	0.08	0.01
	0	0	26	18	4	1
	225	131	231	191	103	224
New Jersey	—	0.07	0.06	0.03	—	—
	0	4	9	4	0	0
	209	139	176	174	120	143
Delmarva Peninsula	—	0.16	0.02	0.01	—	—
	0	6	3	1	0	0
	163	82	104	140	126	45
Virginia and North Carolina	0.08	0.09	0.01	0.01	—	—
	7	3	1	1	0	0
	135	66	76	122	103	37

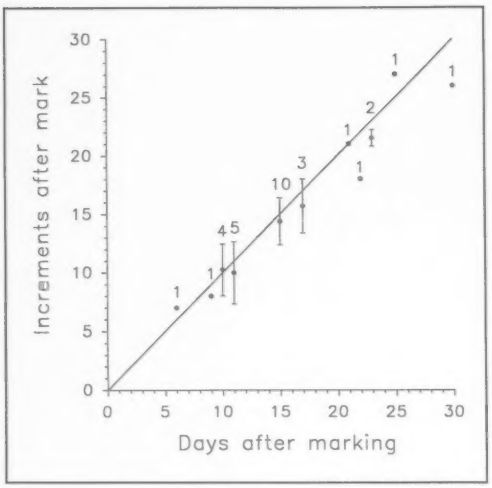

Figure 4
Validation of daily deposition of otolith increments in *Tautoga onitis*, comparing the number of increments outside a tetracycline-induced mark with the number of days since marking. Numbers above data points are numbers of fish tested; error bars are SD's. Resulting regression line does not deviate significantly ($P>0.05$) from a line of one-to-one correspondence.

radius measurements with standard length demonstrated a strong correspondence for all three radii (Fig. 5). For all three cases, a square-root equation provided the best fit.

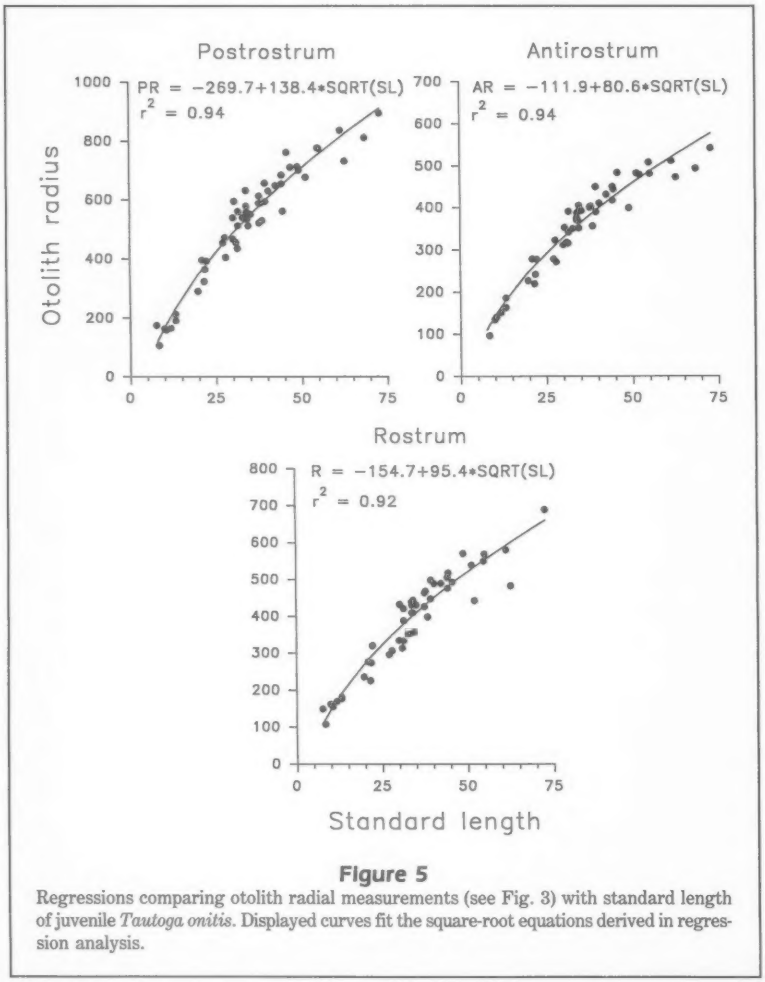

Figure 5
Regressions comparing otolith radial measurements (see Fig. 3) with standard length of juvenile *Tautoga onitis*. Displayed curves fit the square-root equations derived in regression analysis.

Settlement marks and larval stage duration

An obvious transition in the appearance of increments occurred in the sagittae (Fig. 3). Inner increments were generally more distinct because they were higher in contrast, darker in appearance, and more circular than increments outside the transitional area. In the sagittal plane, outer increments diverged in morphology, with increased deposition along the eventual axes of rostrum, postrostrum, and antirostrum. Sagittae of larval tautog (n 5) were comprised of only the darker, inner increments. Thus, we believe this transition in increment contrast and shape takes place at or near the time of settlement, when the individual has completed transformation and moved from a planktonic to epibenthic lifestyle. Settlement marks are a common feature of labrid otoliths, allowing ready distinction of larval and juvenile increments (Victor 1986).

The total number of increments (separated into larval and juvenile stages) was counted for 37 individuals collected in the Great Bay and Little Egg Harbor sampling. The number of increments deposited during the

pelagic larval stage was remarkably similar, with a mean of 20.4 (SD 2.7). Assuming that the first increment is deposited at about the time of hatching, tautog spend 3 weeks in the plankton before settling to the benthos. Subtraction of total increments from the date of collection resulted in a wide spread of estimated birth (hatch) dates, with a mean of 4 June and a range of 17 April–22 July. These dates are consistent with the general timing of the collection of eggs and larvae (Tables 2, 3). Settlement dates, estimated by subtracting only the juvenile-stage increments from the date of capture, were correspondingly widespread, with a mean of 25 June and a range of 6 May–13 August.

Juvenile habitat, size composition, and growth

In throw-trap samples collected in the shallow waters of Great Bay and Little Egg Harbor, juvenile tautog were collected only on vegetated substrates, and were more abundant in sea lettuce (*Ulva lactuca*, *n* 19) than in eelgrass (*Zostera marina*, *n* 2) (Sogard and Able 1991). Juveniles <40 mm in length were rare in the deeper waters sampled by trawls, but the larger young-of-the-year and 1-year-old tautog collected by trawling were most abundant in eelgrass beds. Of 14 sampling stations throughout Great Bay and Little Egg Harbor, two were in eelgrass habitats. These two stations accounted for 69% of the 235 tautog collected by trawling in 1988 and 1989.

Combined length-frequency data from throw-trap sampling and trawling efforts suggested that most tautog in the Great Bay–Little Egg Harbor system, based on these sampling techniques, belonged to one of two year-classes (Fig. 6). Young-of-the-year first appeared in July, primarily in the shallower (<1 m) habitats sampled by throw trapping. In the deeper areas (>1 m) sampled by otter trawl, larger young-of-the-year fishes increased in number in August collections. By September, the young-of-the-year dominated the trawl samples while decreasing in throw-trap sampling.

Modal progression of length-frequency distributions demonstrated relatively rapid growth for both young-of-the-year and 1-year-old tautog during the summer months. In contrast, comparison of young-of-the-year sizes in October with 1-year-old lengths in June indicated only minor growth during the fall, winter, and spring. Juvenile tautog attained a size of 40–100 mm

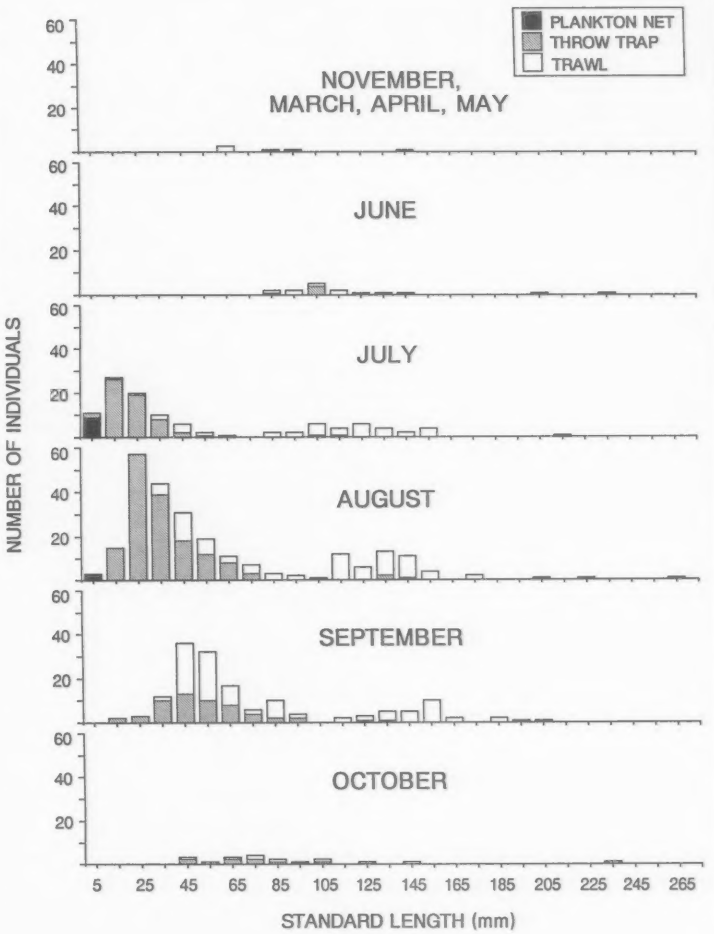

Figure 6

Length-frequency distributions of *Tautoga onitis* collected in the Little Egg Harbor–Great Bay estuarine system. Plankton samples were collected on a weekly basis throughout the year. Throw-trap samples were collected from shallow habitats (<1 m at low tide), May–October; trawl samples were collected from deeper habitats (1–8 m) monthly, with no tautog collected during December–February.

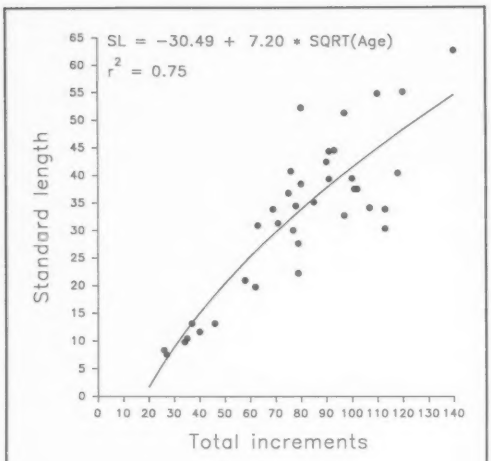

Figure 7
Total number of increments vs. standard length for 37 juvenile *Tautoga onitis*. The plotted square-root equation provided the best fit in regression analyses.

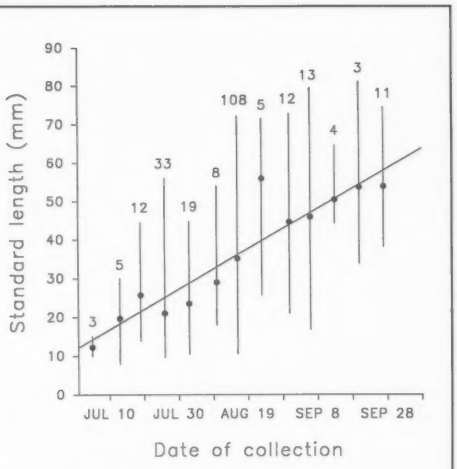

Figure 8
Mean and range in standard length of juvenile *Tautoga onitis* collected on a weekly basis in 1988. All fish were collected with throw traps, primarily from artificial seagrass substrates. The regression line was fit to means for each sampling date (n 13). Numbers above ranges are the number of tautog collected each week.

SL in their first growing season, with a modal size of 75 mm in October (Fig. 6). One-year-old fish reached a size of 110–170 mm SL by the end of their second summer, with a modal size in September of 155 mm.

Comparison of otolith ages (total increment counts) with standard lengths provided a general estimate of juvenile growth. The resulting relationship was best described by a square-root equation (Fig. 7), indicating a slight decline in absolute growth rate with age. If the data are fit to a linear equation, a slope of 0.47 results, thus estimating an average rate of 0.47 mm/day during the early juvenile stage. Substantial variability was evident, especially among older individuals (Fig. 7).

To obtain an estimate of growth based on length-frequency distributions, we compared length with the date of capture for 236 juveniles collected only by throw traps in 1988. When the mean length each week was regressed on time (Julian date), the resulting slope provided an estimated growth rate of 0.52 mm/day (Fig. 8).

Discussion

Spawning patterns

Based on the seasonal occurrence of eggs and larvae, the peak spawning period for tautog in the Mid-Atlantic Bight and inshore New Jersey waters is during the summer. Spawning appears to follow a geographical progression, beginning earlier in the southern part of the region. Consistent with this pattern, Eklund and Targett (1990) report that gonosomatic indices of adult tautog off Maryland and northern Virginia are highest in May.

The egg collections in New Jersey and high egg and larval abundances in areas such as Narragansett Bay (Bourne and Govoni 1988) demonstrate that tautog spawn primarily inside estuaries or nearshore waters. The MARMAP collections indicate that spawning activity involves offshore continental shelf waters as well, since all of the tautog larvae obtained during MARMAP surveys were preflexion stage.

Otolith deposition patterns

Otolith increments of juvenile tautog can be reliably used to obtain valuable age and growth information. The strong correspondence of otolith size (based on radial measurements) with fish size suggests that accurate back-calculation of size-at-age is possible. Increments on the sagittae are deposited on a daily basis and can be readily separated into planktonic and demersal stages, due to the distinct contrast in microstructure at the time of settlement. We did not, however, test increment deposition rates under conditions of poor or negative growth. These conditions have resulted in less than daily increments in other species (Geffen 1982, Lough et al. 1982, McGurk 1984, Alhossaini and Pitcher 1988, Siegfried and Weinstein 1989,

Sogard 1991, Szedlmayer and Able In press), and we caution that this may also be the case for tautog otoliths.

Settlement

Increment counts preceding the settlement mark averaged 20.4, suggesting larvae spend approximately 3 weeks in the plankton before settling to the benthos. This estimate of larval stage duration is similar to that derived by Victor (1986) for a sample of five tautog ($\bar{x}$ 25.4). The planktonic stage for tautog is relatively short compared with other labrids; Victor (1986) estimated average larval durations of 17–104 days for other wrasse species.

The earliest estimated date of settlement, based on otolith increments, was earlier than the first collections of juveniles with throw traps, suggesting that tautog were not available to the collecting gear during and immediately after settlement. The smallest juveniles for which we have otolith information were 7.6–13.2 mm SL and had 11–23 increments ($\bar{x}$ 16.3) deposited after the settlement mark. Victor (1983) reported that newly settled wrasses of the species *Halichoeres bivittatus* bury in sediments immediately following settlement from the plankton and remain buried for an average of 5 days. We do not know if a similar behavior occurs in *Tautoga onitis*.

Juvenile habitat utilization

Our collection of juvenile tautog primarily in vegetation is in accord with prior studies, which demonstrated an association with structured habitats (Olla et al. 1974, Olla et al. 1979). Several studies comparing eelgrass vs. unvegetated substrates noted significantly higher densities of tautog in grassbeds, with few or no tautogs collected on bare substrates (Briggs and O'Connor 1971, Orth and Heck 1980, Weinstein and Brooks 1983, Heck et al. 1989). The importance of sea lettuce as a nursery habitat has received only limited attention, although Nichols and Breder (1926) mentioned its attraction to small juvenile tautog. In a separate study that also quantitatively compared sea lettuce and eelgrass habitats in New Jersey, using suction sampling, Able et al. (1989) also noted higher abundances of early juvenile tautog in sea lettuce patches than in eelgrass, although the total catch was relatively small. Larger juveniles make extensive use of rocky reef habitats (Olla et al. 1979). The importance of hard substrates for newly settled tautog has not been examined.

All of the smaller juvenile tautog (<35 mm SL) that we collected were from sea lettuce patches or artificial seagrass plots. These individuals were a brilliant green in color. As noted by Nichols and Breder (1926), this color closely matches that of *Ulva lactuca*, but presumably would be conspicuous on a bare sand substrate. In our sampling, these early juveniles were absent from eelgrass beds. The larger juveniles collected during trawl sampling (in eelgrass and other habitats) had a dark, mottled coloration similar to that of the adults as depicted by Bigelow and Schroeder (1953).

Over the course of our summer sampling, we observed a shift in concentration of young-of-the-year from the shallow areas sampled by throw traps to deeper waters sampled by otter trawl (Fig. 6). This shift suggests that newly-settled juveniles concentrate in shallow waters, moving to deeper sections of the estuary with growth.

Although trawling was conducted year round, individuals of age 1 or older were common only from June through September. This pattern could result from inaccessibility to the gear. Some individuals may move out of shallow habitats in the fall to deeper areas of the estuary with more stable sheltering refuges. Behavioral responses displayed by tautog in cold temperatures, i.e., dormancy and remaining in close contact with sheltering structure (Olla et al. 1974) or burying in sediments (Olla et al. 1979), would also reduce capture rates in winter. In addition, some individuals may leave the estuary to winter offshore, although Olla et al. (1974) suggest that most tautogs less than 4 years old remain inshore.

Tautogs older than 1 year may be more abundant in the estuary than trawl catches would indicate. Larger individuals inhabit holes and crevices of eroding salt marsh banks, and other physical structures such as pilings and rock jetties, where they would not be available to trawling gear.

Juvenile growth

Our estimates of sizes attained by juvenile tautog at the end of the first and second summers are larger than the mean lengths (TL) at ages 1 and 2 calculated for Rhode Island tautog from opercular bone annuli (Cooper 1967). Warmer temperatures in New Jersey may support faster mean growth rates than in Rhode Island. In addition, more southern estuaries in the tautog's range have an extended summer season, allowing both earlier spawning in the spring and continued rapid growth prior to declining water temperatures in the fall.

Analysis of length progressions and otolith ages resulted in two similar estimates of natural growth rates for juvenile tautog (0.52 mm/day and 0.47 mm/day). Individual growth rates of juvenile tautog were also measured in the field in caging experiments (Sogard In press). To summarize results of Sogard

(In press), growth rates varied significantly, depending on location in the estuary and habitat type (vegetated or unvegetated). Across four experiments and a total of 141 tautog, growth averaged 0.18 mm/day, with a range of −0.47 to +0.84 mm. At the site (Great Bay 1) and habitat (sea lettuce) supporting the fastest growth, the mean rate was 0.45 mm/day. Thus, length-frequency patterns and otolith ages reported in this study provided growth estimates that were higher than the overall average in caging experiments but comparable to rates for tautog caged in the best habitats. Based on throw-trapping results, juvenile tautog were rare at those sites and habitats where growth in cages was poor (Sogard In press). Thus, for the areas where tautog were likely to be common, the directly measured growth rate in cages was comparable to rates indirectly calculated for unrestrained fishes. The three methods together estimated a rapid growth rate of about 0.5 mm/day for southern New Jersey estuaries during the first summer.

Acknowledgments

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Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf

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Abstract. – Heceta Bank is a large reef on the edge of the central Oregon continental shelf that supports a wide variety of commercial fisheries. Using the research submersible *Delta*, we studied fish abundances on Heceta Bank and the relationship between species composition of fish assemblages and bottom types. Cluster analysis indicated that fish assemblages were most unique on mud, boulder, rock ridge, mud and cobble, and mud and boulder substrates. Rockfishes, particularly pygmy *Sebastes wilsoni*, sharpchin *S. zacentrus*, rosethorn *S. helvomaculatus*, and yellowtail *S. flavidus*, were the most abundant fishes and dominated all substrates except mud, where Dover sole *Microstomus pacificus* and zoarcids *Lycodes pacificus* were most abundant.

Principal component analysis (PCA) and canonical correlation analysis (CCA) were used to determine the sources of variation within the data. PCA demonstrated that habitat variability was a fundamental cause of heterogeneity among fish assemblages. In contrast, CCA showed how species occurrences were related to specific substrates.

Ontogenetic shifts in behavior and substrate preference occurred in pygmy rockfish. Small juveniles often formed dense schools above the bank's shallower rocky ridges. Larger individuals occurred in nonpolarized assemblages on the bottom in cobble and boulder fields.

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Heceta Bank is a major commercial fishery zone off central Oregon. It supports a wide variety of fisheries: a demersal trawl fishery for many species of flatfishes; a longline fishery for halibut *Hippoglossus stenolepis*; midwater trawl and vertical longline fisheries for rockfishes (*Sebastes* spp.); a midwater trawl fishery for hake *Merluccius productus*; and during upwelling, a troll fishery for salmon (*Oncorhynchus* spp). Despite its importance to commercial fisheries, little was known about Heceta Bank prior to our 1987 submersible studies (Pearcy et al. 1989). From those exploratory dives we learned that (1) the bank is composed of diverse substrates, each supporting fish assemblages differing in species composition and relative abundances; (2) shallow areas of the bank act as a nursery for juvenile rockfishes; and (3) commercially valuable species of rockfish are associated with the shallow bank top in untrawlable areas, which thus serve as refugia from most commercial fishing.

Our 1987 studies focused on initial exploration and description of the Bank. Here we report results from our 1988 submersible-based surveys in which we again studied the fishes occurring on the Bank, concentrating specifically on their associations with various bottom types. We selected sampling stations that represented the range of habitats described by Pearcy et al. (1989) (Fig. 1). Our objectives were to (1) further develop methods of collecting and analyzing data that could be gathered from a submersible to study rocky banks; (2) identify the species occurring on Heceta Bank and estimate their relative and absolute abundances; (3) obtain detailed information about the variability of bottom types occurring within each station; and (4) assess the composition of fish assemblages in relation to different bottom types.

Methods

Data collection

We used the submersible *Delta* to make 18 dives at six stations on Heceta Bank in September 1988 (Fig. 1). These stations represented all substrates and depths within range of the submersible (to 366 m).

At each station we made three daylight dives, each by a different observer (DS, MH, WB). Dives began and ended at least an hour after dawn and an hour before sunset, respectively, minimizing the possible effects of diurnal migration by fishes. Almost all dives at each station were made on the same day.

Our methods basically follow those developed for use by scuba divers working on shallow reefs (Brock 1954, Ebeling 1982). Each observer made two 30-minute visual belt transects during each dive, yielding 6 transects per station (i.e., a total of 36 transects, 12 by each observer). To determine if there were any discernible effects from lights or motor noise of the submersible on the fishes, a 10-minute rest was taken with all lights and machinery off between each pair of transects. To minimize variability caused by within-transect substrate changes, all transects within a station started as closely as possible at the same position, as determined by Loran C. However, due to limits in the accuracy of Loran C and variability in current speed and direction, transects within stations were usually 100–300 m apart.

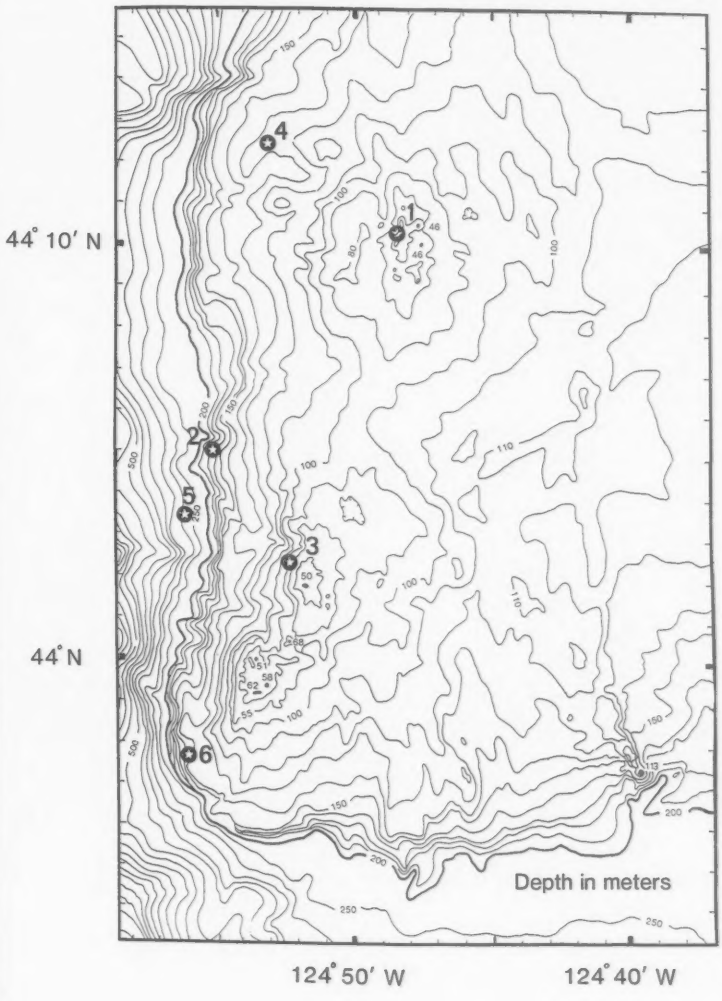

Figure 1
Bathymetric chart of Heceta Bank, Oregon, indicating locations of the six stations sampled.

The observer in the submersible viewed the bottom through a single bow port which limited observation to about a 90° view. Submersible altitude above bottom (at height of observers' eyes from the bottom) was held as closely as possible to 2 m, as measured by an altimeter on the vehicle and by a chain suspended from the submersible (see below). Widths of the viewing path at altitudes of 0.5–2.0 m were determined empirically by "flying" the vehicle at right angles across a decimeter-striped 3 m pole placed on the bottom and noting the length of the pole visible to the observer between two fixed points on the submersible. At 2 m altitude, the transect width was 2.3 m. Thus, the density of fishes (no./m^2) was calculated as the number of fishes seen along a transect divided by 2.3 times the transect length in meters. To aid in estimating fish length and maintaining vehicle altitude, an ~0.4 m long fiberglass rod, striped in alternating black and white decimeters, was hung by chain from the vehicle within the observer's view. Chain length was adjusted so that when the rod was just above the bottom, the observer's altitude was 2 m.

The goal of the observer during a dive was to identify, count, and estimate the lengths (to the nearest decimeter) of all fishes seen along the transect. Fishes were categorized into "schooling" when five or more individuals formed a polarized group (i.e., all fish

moving syncronously in the same direction). Non-polarized aggregations or solitary individuals were considered "non-schooling." Data were collected by continuous audio tape recordings of the observer during transects, continuous video records (also including audio, time, and date), and 35 mm still photographs automatically triggered every 30 seconds. We used a PhotoSea 1000 35 mm still camera and a PhotoSea 2000 video camera, both on fixed mounts outside the vehicle. The video camera was mounted on the starboard bow of the submersible and recorded a field of view that partially overlapped that of the observer within the submersible. The audio track of the videotape recorded the observers comments which allowed real-time integration of fish observations and bottom-type descriptions (see below). Visibility always extended at least to the limits illuminated by the lights (i.e., ~3 m or more except where limited by topography). Immediately following each dive, data were entered by computer into a relational database system and verified against the audio tapes.

We tried to minimize inherent biases of submersible studies as suggested by Ralston et al. (1986), such as fishes not seen or unidentified, diurnal variability, and effects of vehicle on fishes. Through a detailed analysis of fish and bottom-type observations recorded in the continuous video coverage of each transect, several observer-related factors affecting data collection were discovered. First, the diving observer usually noted fishes first, then bottom type. When fishes were present coincidentally with a substrate change, fish records were frequently correlated with the wrong bottom type. Second, observers tended to record substrate types based upon larger (high-relief) features rather than small (low-relief) ones, even when the smaller ones were preponderant. Apparently, boulders impressed observers more than cobble or mud, even when the latter were most abundant. Neither of these sources of error was intuitively obvious or suspected. If left uncorrected, these errors would have changed the apparent fish-substrate associations.

Due to these inherent biases, we extracted data on bottom types from the videotape record of each transect. In order to standardize any bias in the evaluation of bottom types, a single observer (BT) reviewed all videotapes. Dominant substrates were categorized using a two-code combination of seven possible categories: mud (code M), sand (S), pebble (P, diameter <6.5 cm), cobble (C, >6.5 and <25.5 cm), boulders (B, >25.5 cm), flat rock (F, low vertical relief), or rock ridges (R, high vertical relief). Substrate was noted as either "primary" if it covered at least 50% of the area viewed (the first code), or "secondary" if it covered more than 20% of the area viewed (the second code). For example, a mud-boulder bottom type (code MB) consisted of at least 50% cover by mud with at least 20% cover by boulders. In contrast, a mud bottom (MM) consisted of >80% cover by mud.

We defined each transect segment of uniform bottom type as a "habitat patch." Transects within stations were therefore represented by a series of habitat patches defined by the frequency of substratum change along a transect. As a result, the size of habitat patches varied both within and among transects in conjunction with the area of uniform bottom types. The average habitat patch measured 150.8 m^2 (SE 15.4 m^2, n 524).

Data analysis

Although data were collected on all observed fish, data analysis focused on the distribution and abundance of non-schooling fishes rather than schooling fishes, because data for the former were more reliable. First, due to the lack of a manipulator on the submersible, we were unable to collect schooling fishes, which were typically small and unidentifiable, to obtain voucher specimens for positive identification. Second, schooling species were generally more abundant above the bottom in midwater and were not common in the transect path.

We tested for statistical differences among stations and observers in non-schooling fish abundance using a nested two-factor analysis of variance (ANOVA). Thirty-minute transect segments served as nested replicates. Sample variances were examined for homogeneity using Bartlett's test (Sokal and Rohlf 1981) prior to using the ANOVA. Because the raw data were heteroscedastic, the analysis examined the log-transformed total abundance of non-schooling fish per m^2.

To examine the variation in fish assemblages among transects, data were analyzed using principal component analysis (PCA). The PCA was an R-mode analysis of the variance-covariance matrix based on the log-transformed abundance of non-schooling fish per m^2. By definition, the axes examined in PCA are statistically independent of on another (Pimentel 1979). Rare species were eliminated from analysis by selecting only species present on at least 10 of the possible 36 transects. A total of 30 taxa met this criterion and were used in the analysis.

To examine the overall similarity of fish assemblages occurring on different substrates, data were analyzed using hierarchical cluster analysis. The analysis was limited to 21 species which were present on at least 12 of the possible 36 transects. The data in this analysis were the log-transformed total number of individuals per m^2 of each species that occurred on each substrate combination. A dendrogram was constructed using

Euclidean distance as a measure of similarity and the group-average clustering method (Pimentel 1979).

To examine specific associations between fish abundance and bottom-type characteristics, data were examined using canonical correlation analysis (CCA). CCA maximizes correlations among two sets of variables while it minimizes correlations within sets (Pimentel 1979). We used CCA to quantify associations between abundances of non-schooling fish species (data set 1) and bottom types (data set 2). Our primary goal was to extract meaningful, natural associations between fishes and habitat factors potentially influencing their distribution and abundance. CCA estimates these associations using four metrics (Pimentel 1979). First, the *canonical correlation* measures the overall association between the two data sets. Second, the *redundancy coefficient* measures the amount of overall variation in one data set as predicted by the other. While the canonical correlation coefficient describes the goodness-of-fit of the two data sets, which can be influenced by a single high correlation between one variable in each data set, the redundancy coefficient measures the extent of overlap in the variation of the two data sets. Third, the *variable loadings* indicate which variables are correlated on a particular axis. The fourth metric, *canonical variate scores*, measures the contribution of each sampling unit (in this analysis, the habitat patch) to the fish-habitat pattern depicted on each axis. Canonical variate scores are derived for each data set: scores for the habitat data indicate the relative cover of specific bottom types on each axis, while scores for the fish data indicate the relative abundance of specific fish on each axis. Canonical variate scores derived from CCA represent a powerful way to measure the abundance of fish in reference to habitat type. In essence, the method controls for the effects of sampling across a range of different habitats, and thus increased our power to detect meaningful spatial variation in fish abundance.

Data for CCA were derived using observations of habitat patches, which were discrete segments of uniform bottom type within each transect (n 524 segments for all transects). For each habitat patch, the abundances of 21 fish species were tabulated relative to the summed total area (in m^2) comprised by the habitat. For mixed bottom types, the total patch area was apportioned 80% to the primary substrate and 20% to the secondary substrate.

Results

The six stations represented a wide variety of substrates, ranging from shallow rocky ridges separated by sand, to intermediate-depth cobble and boulder fields, to deep mud and pebble bottoms (Figs. 1,2). Stations 1 and 3 (shallow bank tops) were rocky ridges at 60–80 m depth separated by sand and boulder-filled valleys; station 2 (bank saddle) was primarily mud with interspersed cobble at 150–200 m; station 4 was mud, ridge, and cobble at 145–175 m; station 5 was mud at 250–340 m; and station 6 was boulder and cobble grading into mud at 200–270 m. Because transects were always run into the current to insure controllability of the vehicle, distance traveled along the transects was not standardized, but was in the range 467–2367 m ($\bar{x}$ length 1357 m, SE 460 m).

Nested two-way ANOVA of transects and observers, based on the relative abundances of all non-schooling fish species summed, indicated significant differences among stations (F 6.22, df 5,18, $P<0.01$), but not among observers (F 1.39, df 2,18, $P>0.05$), or in interactions among observer transects and stations (F 0.48, df 10,18, $P>0.05$). A Student-Newman-Keuls multiple-range test separated the mean number of non-schooling fish at stations into two subgroups: station 4, where fish were most abundant at 2.09 fish/m^2, and all other stations, which ranged between 1.84 fish/m^2 (station 6) and 0.31 fish/m^2 (station 1).

Species identified: Number and size

We identified 38 taxa to species in our 1988 dives. This represents a 23% increase over the 31 species identified in 1987 (Pearcy et al. 1989). The increase was due primarily to species that were uncommon, suggesting that we identified most or all of the numerically important species on Heceta Bank. There were distinct differences in taxonomic composition and abundances between non-schooling and schooling fishes. About 89% of the non-schooling fishes seen were identified to species; fewer than 2% were not identified to family or genus. All schooling fishes seen were *Sebastes*. Of these, only 49% were identified to species; the remainder were identified to genus only (Table 1). Most of the schooling fish were small or juvenile fish that we could not identify without voucher specimens.

We counted 10,102 non-schooling fish, ranging from 3829 individuals of pygmy rockfish *Sebastes wilsoni* to one individual in each of ten species (Table 1). Schooling fishes comprised 22,470 individuals, over 50% of which (12,820) were unidentified small *Sebastes*. The most abundant identifiable schooling species was again the pygmy rockfish, with 8390 individuals. The least-abundant schooling species was widow rockfish *Sebastes entomelas* with 20 counted. The total number of fish schools seen (all species) was 145, ranging from 70 pygmy rockfish schools to one school of widow rockfish. The number of individuals per school ranged from about 10 to 330.

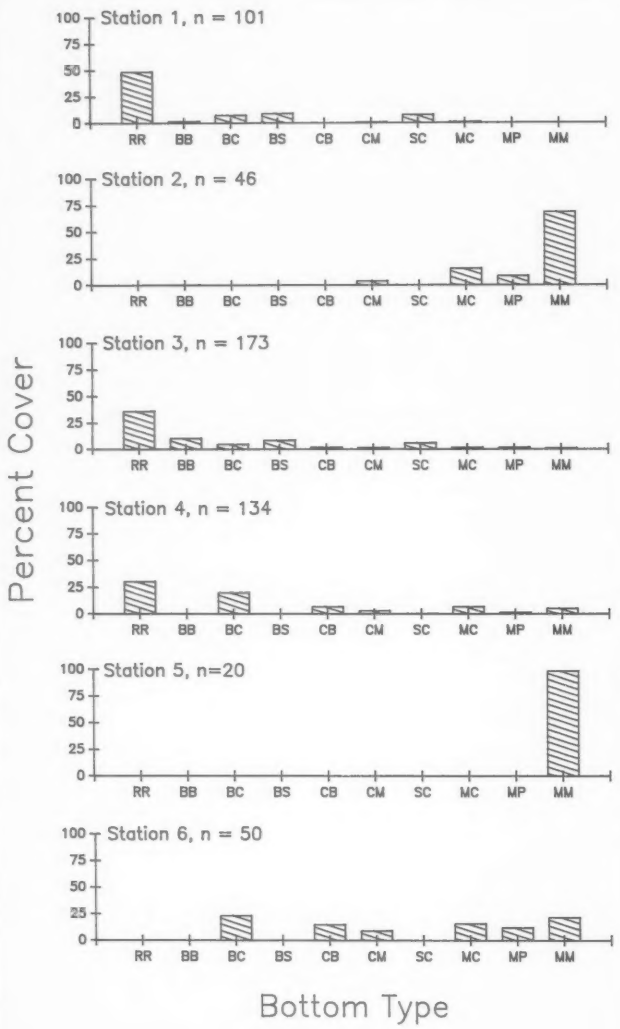

Figure 2

Percent cover of the ten most abundant bottom-type combinations at Heceta Bank, Oregon. RR = rock ridge; BB = boulder; BC = boulder–cobble; BS = boulder–sand; CB = cobble–boulder; CM = cobble–mud; SC = sand–cobble; MC = mud–cobble; MP = mud–pebble; MM = mud (see text for a description of bottom-type codes). n = number of habitat patches sampled per station.

Among non-schooling species, the estimated total length ranged from 105 cm (dogfish shark *Squalus acanthias*) to a mean of 12 cm (unidentified small *Sebastes*) (Table 1). Many smaller fishes were seen, but could be identified only to genus (*Sebastes* juveniles) or family (Gobiidae). Among schooling species, average length varied from 42 cm (yellowtail rockfish *Sebastes flavidus*) to 11 cm (*Sebastes* juveniles).

Ontogenetic habitat changes

Several rockfish species occurred both in schools and singly, including pygmy, yellowtail, sharpchin *S. zacentrus*, redstripe *S. proringer*, and canary *S. pinniger*. Pygmies were the single-most abundant species identified in either category. Schools of pygmy rockfish consisted of significantly smaller individuals, averaging 16.1 cm, whereas non-schooling aggregations and solitary individuals averaged 19.4 cm TL (ANOVA, F 18.0, df 1,699, $P<0.01$). Furthermore, schools were usually associated with ridge tops shallower than 100 m, while non-schooling fish were on cobble and boulder bottoms at depths of 100–150 m. A similar analysis of the data for yellowtail, sharpchin, redstripe, and canary rockfish showed no significant difference between sizes of individuals in and out of schools (ANOVA, all $P>0.05$).

Differences among stations: Fish assemblages

Results of the PCA indicated striking differences among stations in both the composition of fish assemblages and the similarity of individual transects within stations (Table 2, Fig. 3). Bartlett's sphericity test indicated that the first two axes described significant non-random patterns of variation among species, and accounted for 70% of the total variation. The first axis, which accounted for 49% of the variation, primarily contrasted transects at station 4 (intermixed mud and rocky ridges) vs. transects at station 5 (mud) (Fig. 3). Transects from stations 1 and 3 (shallow rocky bank tops) formed intermediate homogeneous groups, while transects from stations 2 and 6 (medium-depth boulder and cobble fields) formed intermediate heterogenous groups. Variable loadings indicated that this axis primarily contrasted variation in the relative abundance of rosethorn, pygmy, canary, sharpchin, yellowtail, and greenstriped rockfish, which were abundant at stations 1, 3, and 4 with the relative abundance of thornyhead rockfish, rex sole, sablefish, poachers, and zoarcids, which were abundant at station 5 (Table 2).

Table 1

Numbers of individuals, average total lengths, and standard errors of lengths for schooling and non-schooling fish species identified on Heceta Bank, Oregon, September 1988.

Species	No. seen	Mean length (cm)	SE
Schooling			
Unident. small rockfish (*Sebastes* spp.)	12820	11.1	1.02
Pygmy rockfish (*S. wilsoni*)	8390	16.1	0.72
Yellowtail rockfish (*S. flavidus*)	590	42.3	1.94
Sharpchin rockfish (*S. zacentrus*)	320	24.1	2.38
Redstripe rockfish (*S. proriger*)	220	25.0	4.73
Canary rockfish (*S. pinniger*)	110	41.7	4.70
Widow rockfish (*Sebastes entomelas*)	20	35.0	*
Non-schooling			
Pygmy rockfish (*S. wilsoni*)	3829	19.4	0.23
Sharpchin rockfish (*S. zacentrus*)	2030	23.7	0.28
Rosethorn rockfish (*S. helvomaculatus*)	931	21.6	0.10
Dover sole (*Microstomus pacificus*)	436	30.3	0.37
Unident. sculpins (Cottidae)	319	15.8	0.09
Shortspine thornyhead (*Sebastolobus alascanus*)	310	21.7	0.32
Blackbelly eelpout (*Lycodes pacificus*)	307	25.4	0.29
Greenstriped rockfish (*Sebastes elongatus*)	288	26.5	0.33
Unident. poachers (Agonidae)	248	22.5	0.15
Slender sole (*Lyopsetta exilis*)	240	22.5	0.16
Unident. small rockfish (*Sebastes* spp.)	130	11.6	1.35
Yellowtail rockfish (*S. flavidus*)	126	43.6	0.62
Rex sole (*Glyptocephalus zachirus*)	120	27.3	0.49
Unident. flatfish (Pleuronectidae)	93	21.3	1.21
Canary rockfish (*S. pinniger*)	78	46.9	0.98
Thornback sculpin (*Paricelinus hopliticus*)	57	14.8	0.05
Spotted ratfish (*Hydrolagus colliei*)	54	44.1	0.53
Unident. fish	47	18.2	1.30
Unident. large rockfish (*Sebastes* spp.)	47	23.1	0.94
Redstripe rockfish (*S. proriger*)	38	29.0	1.14
Ronquils (Bathymasteridae)	33	14.7	0.16
Sablefish (*Anoplopoma fimbria*)	33	54.7	3.53
Kelp greenling (*Hexagrammos decagrammus*)	29	32.2	0.64
Non-schooling (continued)			
Yelloweye rockfish (*S. ruberrimus*)	27	45.4	1.78
Petrale sole (*Eopsetta jordani*)	26	27.3	0.55
Threadfin sculpin (*Icelinus filamentosus*)	26	23.5	0.52
Longnose skate (*Raja rhina*)	23	72.8	40.6
Sandpaper skate (*R. kincaidii*)	22	30.0	2.77
Lingcod (*Ophiodon elongatus*)	20	46.5	9.96
Blacktail snailfish (*Careproctus melanurus*)	15	30.3	0.69
English sole (*Parophrys vetulus*)	15	32.3	1.65
Splitnose rockfish (*S. diploproa*)	13	31.9	2.03
Black eelpout (*Lycodes diapterus*	13	28.1	1.10
Redbanded rockfish (*S. babcocki*)	11	28.6	3.78
Eared blacksmelt (*Bathylagus ochotensis*)	11	15.0	*
Big skate (*R. binoculata*)	10	68.0	32.4
Hagfish (*Eptatretus* sp.)	10	34.0	3.83
Unident. blennies (Blenniidae)	6	15.0	*
Bocaccio (*S. paucispinis*)	5	53.0	3.13
Sculpin (*Icelinus* sp.)	4	27.5	1.25
Tiger rockfish (*S.nigrocinctus*)	4	40.0	1.67
Sanddab (*Citharichthys* sp.)	3	15.0	*
Unident. blotched rockfish (*Sebastes* spp.)	3	25.0	*
Eelpout (*Lycodapus* spp.)	2	15.0	*
Arrowtooth flounder (*Atheresthes stomias*)	1	45.0	—
Darkblotched rockfish (*S. crameri*)	1	35.0	—
Spiny dogfish (*Squalus acanthias*)	1	105.0	—
Unident. smelt (Osmeridae)	1	15.0	—
Pacific Ocean perch (*S. alutus*)	1	25.0	—
Pacific cod (*Gadus macrocephalus*)	1	55.0	—
Sand sole (*Psettichthys melanostictus*)	1	35.0	—
Silvergray rockfish (*S. brevispinis*)	1	55.0	—
Unident. eelpout (Zoarcidae)	1	35.0	—
Unident. skate (Rajidae)	1	15.0	—

*No observed variation; all fish estimated to be same length.

The second axis, which described 20% of the variation of relative fish abundance, presented an additional independent pattern of variation among stations (Table 2, Fig. 3). This axis primarily contrasted transects at stations 1 and 3 (shallow rock ridge) with transects from all other stations. As in the first axis, transects within stations along the second axis were heterogeneous; that is, the relative abundances of the fishes seen varied among transects. Station 1 transects were relatively homogeneous compared with transects at stations 2, 3, and 6, which varied considerably. Variable loadings indicated that this axis represented variation in the relative abundance of kelp greenlings and lingcod, which were abundant on bank tops, versus thornyhead and sharpchin rockfish, zoarcids, threadfin sculpin, and dover, rex, and slender sole, which were abundant at other stations.

Fish-habitat associations

Of the 49 possible combinations of bottom type (7×7 types), 27 were encountered. Cluster analysis indicated that habitat types had varying degrees of similarity in fish assemblages (Fig. 4). Mud had the most distinct

Table 2

Results of principal component analysis. Underlined bold characters indicate high variable loadings, with positive and negative loadings being inversely correlated along each axis. Thus, PC1 depicts a gradient from soft-bottom species (negative loadings) to hard-bottom species (positive loadings). PC2 depicts a secondary gradient from hard-bottom species (negative loadings) to soft-bottom species (positive loadings).

	PC1	PC2
Eigenvalue	3.056	1.266
Percent of total variation	49.3	20.4
Chi-square	1778	1557
Degrees of freedom	434	405
Variable loadings		
Canary rockfish (*Sebastes pinniger*)	**0.826**	0.135
Yelloweye rockfish (*S. ruberrimus*)	0.477	−0.230
Yellowtail rockfish (*S. flavidus*)	**0.657**	−0.092
Redbanded rockfish (*S. babcocki*)	−0.552	0.338
Redstripe rockfish (*S. proriger*)	0.411	0.180
Sculpins (Cottidae)	**0.748**	0.036
Threadfin sculpin (*Icelinus filamentosus*)	0.339	**0.447**
Kelp greenling (*Hexagrammos decagrammus*)	0.189	**−0.621**
Lingcod (*Ophiodon elongatus*)	0.203	**−0.525**
Rosethorn rockfish (*S. helvomaculatus*)	**0.888**	−0.296
Pygmy rockfish (*S. wilsoni*)	**0.892**	0.372
Sharpchin rockfish (*S. zacentrus*)	**0.714**	**0.602**
Splitnose rockfish (*S. diploproa*)	−0.595	0.266
Greenstriped rockfish (*S. elongatus*)	**0.670**	0.286
Shortspine thornyhead (*Sebastolobus alascanus*)	**−0.690**	**0.446**
Eelpouts (Zoarcidae)	**−0.701**	**0.606**
Hagfish (*Eptatretus* sp.)	−0.222	0.385
Spotted ratfish (*Hydrolagus colliei*)	−0.326	**0.461**
Poachers (Agonidae)	**−0.751**	**0.519**
Sablefish (*Anoplopoma fimbria*)	−0.668	0.400
Searchers (Bathymasteridae)	0.441	−0.141
Blacktail snailfish (*Careproctus melanurus*)	−0.641	0.198
Dover sole (*Microstomus pacificus*)	−0.503	**0.761**
English sole (*Parophrys vetulus*)	−0.066	0.140
Petrale sole (*Eopsetta jordani*)	−0.005	0.192
Rex sole (*Glyptocephalus zachirus*)	−0.644	**0.448**
Slender sole (*Lyopsetta exilis*)	−0.180	**0.582**
Big skate (*Raja binoculata*)	−0.179	0.115
Longnose skate (*R. rhina*)	0.311	0.021
Sandpaper skate (*R. kincaidii*)	−0.429	0.238

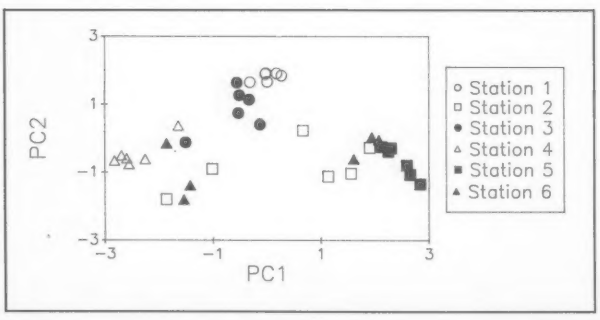

Figure 3

Ordination of first and second principal component scores for 36 transects sampled at six stations on Heceta Bank. The analysis is based on the relative abundances of 30 fish taxa observed (see Table 2 for species list).

fish assemblage, followed by boulder, rocky ridge, mud and cobble, and mud and boulder habitats. In contrast, habitats involving combinations of boulder, mud, sand, and cobble had comparatively similar fish assemblages.

The results of the cluster analysis provide information relevant to the interpretation of the PCA results (Figs. 3, 4). Stations that displayed little among-transect variability in fish assemblages were composed primarily of rocky ridge (stations 1 and 3), and mud (station 5): habitats that had relatively distinct fish assemblages. In contrast, stations with high among-transect variability (primarily stations 2 and 6) were composed of mixtures of mud, cobble, and boulders: habitats sharing relatively similar fish assemblages.

There were additional habitat patterns evident in the distribution of the most abundant rockfish species (Table 3). Comparing abundances of the four most abundant species *within subhabitats*, pygmy rockfish dominated all except mud, mud and cobble, and flat rock. Sharpchin dominated mud and cobble; rosethorn, the flat rock (Table 3). Comparing abundances for each subhabitat *within species*, it is clear that each species, even though it might not be numerically dominant overall, was most abundant in a particular habitat. Thus, pygmy rockfish were most abundant on mud and boulder; sharp chin and greenstriped rockfish on mud and cobble; rosethorn rockfish on boulder; and yellowtail rockfish on rock ridges.

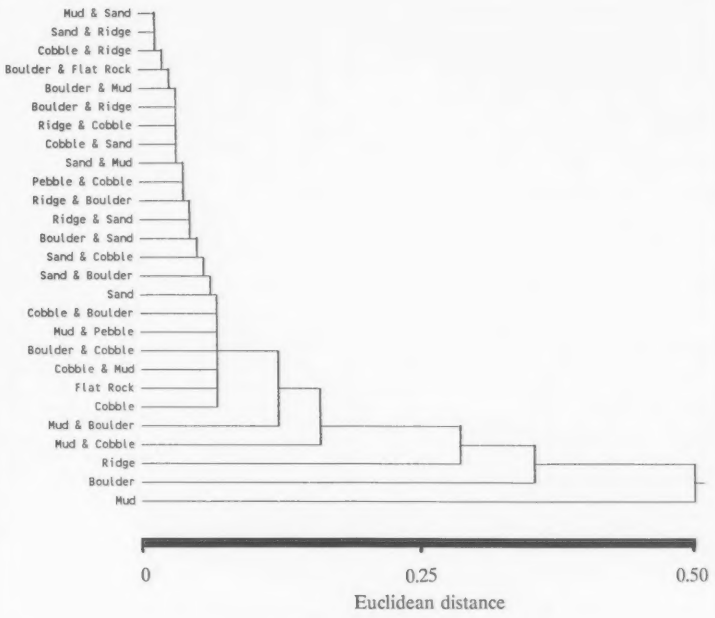

Figure 4

Cluster analysis of all observed bottom types based on the relative abundances of 21 fish taxa (see Table 4 for species list).

In general, the degree of bottom-type relief varied inversely with depth (Fig. 5). High relief substrates such as rock ridges, boulder, and cobble occurred at relatively shallow 80–100 m depths, while low-relief muddy substrates, such as mud and boulder, mud and cobble, and pure mud, occurred relatively deeper, at 160–240 m depths (Fig. 5).

CCA described associations between species abundance and the distribution of specific habitat types (Table 4, Fig. 6). Bartlett's test indicated that the first three axes represented significant canonical correlations. The low values of the redundancy coefficient for these axes (0.10–0.03, measuring variability in fish abundance explained by habitat variation) demonstrated strong correlations between several species and habitats rather than general associations among all species and all habitats.

Table 3

Average number of fish per hectare ($10^4 m^2$) on the seven most distinct habitat types, as determined by cluster analysis (see Fig. 4). Only the 21 most abundant taxa are listed, these taxa used in the canonical correlation analysis. Most-abundant taxon in each category underlined in bold characters. Species absent from a specific habitat are indicated with dashes.

Species	Mud	Mud & cobble	Mud & boulder	Cobble	Boulder	Flat rock	Rock ridge
Agonidae	186	464	1122	–	25	–	18
Bathymasteridae	7	7	–	–	–	–	15
Big skate	7	–	51	–	–	–	–
Canary rockfish	–	14	102	–	–	158	82
Cottidae	24	79	51	67	–	158	73
Dover sole	**499**	343	2295	–	–	–	15
Greenstriped rockfish	64	364	204	266	25	–	79
Kelp greenling	–	–	–	67	76	316	27
Lingcod	–	–	–	67	–	–	30
Longnose skate	7	14	51	–	–	–	6
Pygmy rockfish	21	2129	**8926**	**999**	**2772**	–	**1785**
Redstripe rockfish	–	7	–	–	–	–	43
Rex sole	107	57	1887	–	–	–	–
Rosethorn rockfish	26	343	408	933	161	**474**	675
Sharpchin rockfish	60	**2930**	2754	133	–	–	277
Shortspine thornyhead	239	443	2193	–	–	–	–
Slender sole	76	107	408	–	–	–	–
Spotted ratfish	26	14	510	–	–	–	–
Yelloweye rockfish	–	7	–	–	25	–	27
Yellowtail rockfish	–	29	–	67	176	–	191
Zoarcidae	282	279	1887	–	50	–	18

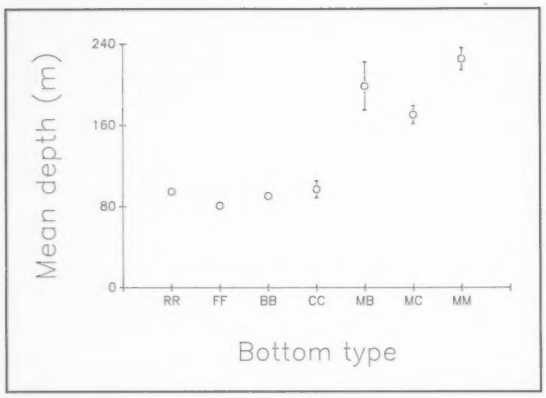

Figure 5
Average depth (±1 SE) of the eight most distinct bottom type combinations on Heceta Bank, Oregon. Bottom codes and sample sizes are as follows: RR = rock ridge (n 109); FF = flat rock (n 4); BB = boulder (n 29); CC = cobble (n 8); MB = mud–boulder (n 11); MC = mud–cobble (n 45); MP = mud–pebble (n 26); MM = mud (n 55) (see text for a description of bottom type codes). n = number of habitat patches sampled per station.

Table 4
Results of canonical correlation analysis. Variables with high loadings are indicated in underlined boldface characters. High negative loadings on the first canonical axis, CC1, indicate fish that were abundant in mud habitats. Similarily, high loadings on CC2 and CC3 indicate fish that were abundant on cobble–boulder bottoms and rock ridge–sand valley bottoms, respectively.

	CC1	CC2	CC3
Canonical correlation	0.849	0.786	0.489
Chi-square	1197	656	249
Degrees of freedom	147	120	95
Fish	Canonical variate loadings		
Canary rockfish (*S. pinniger*)	0.032	**−0.278**	0.090
Yelloweye rockfish (*S. ruberrimus*)	0.035	**−0.382**	−0.139
Yellowtail rockfish (*S. flavidus*)	0.048	−0.021	**0.434**
Redstripe rockfish (*S. proriger*)	0.015	−0.218	−0.098
Cottidae	0.029	−0.200	**0.360**
Kelp greenling (*Hexagrammos decagrammus*)	0.048	−0.140	0.102
Lingcod (*Ophiodon elongatus*)	0.017	−0.134	**0.367**
Rosethorn rockfish (*S. helvomaculatus*)	0.026	**−0.842**	0.295
Pygmy rockfish (*S. wilsoni*)	−0.007	**−0.571**	0.012
Sharpchin rockfish (*S. zacentrus*)	−0.075	**−0.837**	−0.052
Greenstriped rockfish (*S. elongatus*)	−0.155	−0.037	**0.618**
Shortspine thornyhead (*Sebastolobus alascanus*)	**−0.461**	0.066	−0.104
Zoarcidae	**−0.696**	0.077	−0.080
Spotted ratfish (*Hydrolagus colliei*)	−0.337	**−0.504**	−0.172
Agonidae	**−0.678**	0.079	−0.020
Bathymasteridae	0.027	0.043	0.080
Dover sole (*Microstomus pacificus*)	**−0.951**	0.028	−0.005
Rex sole (*Glyptocephalus zachirus*)	**−0.665**	0.065	−0.086
Slender sole (*Lyopsetta exilis*)	−0.088	0.047	−0.081
Big skate (*Raja binoculata*)	−0.324	0.037	−0.059
Longnose skate (*Raja rhina*)	−0.048	0.069	−0.129
Variance extracted	0.132	0.113	0.051
Redundancy	0.095	0.070	0.012
Habitat			
Mud	**−0.998**	0.052	−0.017
Sand	0.037	0.041	**0.665**
Pebble	−0.013	0.070	−0.023
Cobble	−0.041	**−0.514**	0.269
Boulders	0.026	**−0.925**	−0.159
Flat Rock	0.020	0.026	−0.060
Rocky Ridge	0.095	−0.007	**0.529**
Variance extracted	0.144	0.161	0.118
Redundancy	0.104	0.100	0.028

Because bottom-type changes were highly correlated with changes in depth (Fig. 5), the CCA did not confound species associations with bottom types from different depths. Each axis measured associations occurring within the depth range of the habitat indicated by the variable loadings on each axis.

The first axis described variation in fish abundance associated with mud habitats (160–240 m). Variable loadings indicate that thornyheads, zoarcids, poachers, and rex and Dover sole commonly occur on mud (Table 4). Canonical variate scores on this axis were significantly different among stations in both the habitat and fish scores: station 5, the only pure mud station (Fig. 2), was significantly different from all others (Kruskal-Wallis, $p<0.01$) (Fig. 6A).

The second axis contrasted an additional independent fish-habitat association. Variables loadings indicated that ratfish, and rosethorn, sharpchin, yelloweye, canary, and pygmy rockfish were associated with boulder and cobble fields at 75–100 m depths. Canonical scores for the second axis also differed significantly among stations on both habitat and fish scores: station 6, the station with the highest cover of boulder–cobble (Fig. 2), was significantly different from all other stations (Kruskal-Wallis, $p<0.01$) (Fig. 6B).

The third axis indicated an additional association between fish and habitat. Variables loadings indicated that greenstriped and yellowtail rockfish, lingcod, and cottids were associated with sand

and ridge habitats at 75–100m depths. Canonical variate scores among stations differed on the third axis with respect to habitat scores, but not on fish scores. With respect to habitat, stations 1 and 3, which had the highest amount of sand and ridge cover (Fig. 2), were significantly different from stations 2, 4, and 6 (Kruskal-Wallis, $p<0.01$) (Fig. 6C). In contrast, with respect to fish abundance, stations were highly variable, and not significantly different among stations (Kruskal-Wallis, $p>0.05$) (Fig. 6C).

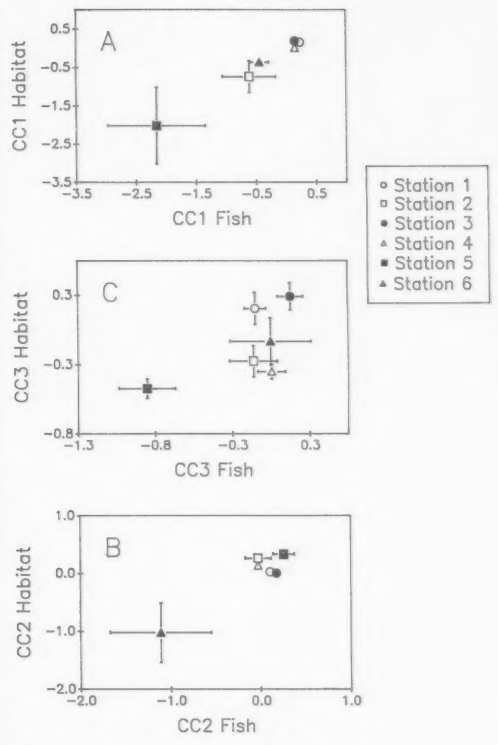

Figure 6
Average canonical variate scores for each station (±1SE) on three canonical correlation axes (see Table 4). Canonical scores for habitat indicate the relative cover of specific bottom types on each axis, while scores for the fish data indicate the relative abundance of specific fish on each axis.

Discussion

The principal objective of our study was to develop methods to estimate spatial variation in fish abundance on Heceta Bank. However, the high variability of bottom types encountered required that we understand the effects of bottom-type variation on fish abundance and distribution.

Fish-habitat associations

The principal components analysis showed that stations with the least variability in fish abundance among replicate transects were those at stations composed of rock ridge, such as the bank tops (stations 1 and 3), and of mud (station 5). In contrast, high variability in fish abundance among replicate transects occurred at stations having combinations of mud, cobble, and boulders (stations 2, 4 and 6). Moreover, canonical correlation analysis indicated that fish assemblages associated with these habitats were unique. Mud, cobble–boulder, and ridge–sand habitats displayed different species composition and relative abundance.

In most sampling situations, such as use of a bottom trawl or bottom-set gillnet, analysis would be limited to a fish-only PCA-type appproach. Within-station variability, such as that documented here, would be largely unaccounted for without detailed information about bottom type. In the present study, canonical correlation analysis of fish abundance relative to bottom type provided key information on a major source of within-station variability.

The ability to estimate bottom-type composition and determine the relationships of species with each substrate is a critical advantage of submersible studies. In shallow water, this has been done using scuba (e.g., Hixon 1980, Larson 1980, Hallacher and Roberts 1985). However, there are few such studies below scuba depths. In the northeastern Pacific, Carlson and Straty (1981) and Straty (1987) used a submersible to study habitat and nursery areas for rockfishes in southeastern Alaska. Straty (1987) concentrated on species of juvenile rockfishes and their occurrence in relation to substrate type and relief; he did not attempt to quantify abundances. Richards (1986) similarly investigated distributions of deep rockfishes at 21–140m and related their occurrence to bottom type. Although she was able to show substrate associations for three species (*Sebastes elongatus*, *S. maliger*, and *S. ruberrimus*), only three substrate categories were used, and abundances of fishes were determined on the basis of distance of maximum visibility. Nevertheless, she recognized the importance of such studies and developed initial methods for obtaining data on this subject.

Abundances of species

We know of no comparable data to that presented here for fish abundances on Heceta Bank. However, similar studies have been done on inshore reefs in central California. Miller and Geibel (1973), using scuba tech-

niques similar to our submersible methods, estimated abundances of juvenile and adult rockfishes along transects on an inshore reef supporting an extensive kelp forest. Their estimates of juvenile abundances are much higher than ours: more than 46,000 fish/ha compared with our maximum of 15,039 fish/ha (station 3). Comparing abundances of adults at the same stations, they estimated 3133–5046 fish/ha vs. 558–1724 fish/ha at our station 3. The maximum estimated number of adult fishes at any of our stations was 9635 fish/ha (station 4). However, our estimates at the shallow bank top stations (1 and 3) are low because they did not include most of the schooling fishes, which were above the submersible. We have no accurate estimates of the abundances of these fishes, primarily yellowtail and widow rockfish. They occurred in schools of thousands.

Availability of comparative data

There are few data sets comparable with ours that were obtained by other methods. Rough bottoms are untrawlable, reducing usable gear to longlines or set nets. Even where these are used, if substrate varies over the length of the longline or net, they "integrate" the fishes over those different bottom types, preventing association of species with specific substrate types. Using otter trawls with foot rope rollers, Barss et al. (1982) studied fish assemblages associated with "rough" (rocky bottom fishable with nets using rollers) and "smooth" bottom on the west (offshore) side of Heceta Bank. The areas with most relief were unfishable (including our stations 1 and 3). They found distinct differences in catches between the two types of areas, but admitted that their results were biased by the type of gear they were forced to use in order to trawl on rough bottom.

Recently, Matthews and Richards (In press) used gillnets to compare fish assemblages on trawlable and untrawlable bottoms west of Vancouver Island. Their goal was to determine whether, as commercial fishermen believe, untrawlable bottom west of Vancouver Island provides refuges for commercially exploited fishes (primarily Pacific Ocean perch) caught nearby. They concluded there were no reservoir populations. However, given the mesh size of their bottom-set gillnets, they were unlikely to sample either juveniles or semipelagic species such as yellowtail and widow rockfish. Thus, given our current and previous observations of juvenile and yellowtail rockfish associated with shallow, high-relief rocky ridges (Pearcy et al. 1989), we suggest that these unfished areas could still provide refuges for fishes in either of those categories.

Habitat shifts

Ontogenetic habitat shifts, such as those desribed here for pygmy rockfish, are common among rockfish species. Westrheim (1970), Carlson and Haight (1976), and Straty (1987) found that juvenile Pacific Ocean perch *Sebastes alutus* were usually shallower than adults. Carr (1983) described the growth-related migration of juvenile *S. atrovirens*, *S. carnatus*, *S. chrysomelas*, and *S. caurinus* to the bottom in a central California kelp forest. However, Hallacher (1977), studying adults and juveniles of *S. mystinus* and *S. serranoides* in Monterey Bay at depths of ~25 m or less, found that abundances of both increased with depth, maxima occurring at the greatest depths sampled. This difference could be related to degree of association with the bottom as adults. The species Carr (1983) studied were benthic as adults, whereas the latter two species occur in the water column.

Conclusions

The results presented here show the utility of using a submersible rather than bottom set nets, traps, or longlines to study fish-substrate associations in deep water areas where substrate is heterogeneous. Other methods, such as Remote Operated Vehicles, rely on video and still camera images, which are not as adequate for accurate identification as the human eye. Moreover, other types of gear do not allow detailed characterization of the substrate sampled, but rather integrate the catch from a variety of habitats. We believe that the methods presented here, in addition to describing basic fish-habitat associations, allowed us to control the effects of sampling across a range of different habitats, and increased our ability to detect meaningful spatial variation in fish abundance.

Acknowledgments

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Management advice from a simple dynamic pool model

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Abstract.—This paper is devoted to a theoretical examination of two rules of thumb commonly used in fishery management: (I) the fishing mortality rate associated with maximum sustainable yield (F_{MSY}) equals the natural mortality rate, and (II) the equilibrium stock biomass at maximum sustainable yield equals one-half the pristine stock biomass. Taken together, these rules of thumb are shown to be inconsistent with any simple dynamic pool model in which three conditions hold: (1) the first derivative of the stock-recruitment relationship is uniformly nonnegative, (2) the second derivative of the stock-recruitment relationship is uniformly nonpositive, and (3) the first derivative of the weight-at-age relationship is uniformly positive. An example of such a model is presented and the equilibrium solution derived analytically. In this model, F_{MSY} can be either greater than or less than the natural mortality rate, while the equilibrium stock biomass at maximum sustainable yield is consistently less than one-half the pristine stock biomass. To illustrate the utility of the theoretical framework developed, the model is applied to the eastern Bering Sea stock of rock sole *Pleuronectes bilineatus*.

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Two rules of thumb

Despite its acknowledged shortcomings (e.g., Larkin 1977), management for maximum sustainable yield (MSY) remains a common strategy among fisheries professionals. Under a constant harvest rate policy, this strategy is implemented by exploiting the stock at the fishing mortality rate corresponding to MSY (F_{MSY}). Alternatively, this strategy could be implemented by exploiting the stock so as to maintain its biomass at the level corresponding to MSY, $B(F_{MSY})$. To estimate F_{MSY} and $B(F_{MSY})$, fishery scientists and managers employ a variety of approaches, ranging from highly sophisticated simulation models to simple "rules of thumb." Frequently used examples of the latter can be found in the form of two hypotheses employed by Alverson and Pereyra (1969) in their analysis of the potential yield of certain fish stocks. These hypotheses (hereafter referred to as Rules I and II) are

$$\frac{F_{MSY}}{M} = 1 \qquad \text{(I)}$$

and

$$\frac{B(F_{MSY})}{B(0)} = 0.5, \qquad \text{(II)}$$

where F is the instantaneous rate of fishing mortality per year, F_{MSY} is the value of F that produces MSY in equilibrium, M is the instantaneous rate of natural mortality per year, B(F) is the equilibrium stock biomass corresponding to a fishing mortality rate of F, $B(F_{MSY})$ is the equilibrium stock biomass when $F = F_{MSY}$, and B(0) is the pristine stock biomass (i.e., equilibrium stock biomass when $F = 0$).

Alverson and Pereyra (1969) presented a sketchy derivation of Rules I and II, leaving open the question of which models might be capable of leading to the hypothesized relationships. A number of authors have subsequently examined specific models in this context and shown them to be inconsistent with Rules I and II. Gulland (1971) and Beddington and Cooke (1983) cast doubt on the robustness of Rules I and II in terms of their applicability to the "simple" model of Beverton and Holt (1957), but did not generalize their conclusions beyond that particular model. Likewise, Francis (1974) demonstrated inconsistencies between Rules I and II and a set of assumptions derived from the Schaefer (1954) model, although his argument was weakened somewhat by computing MSY in terms of numbers, not biomass. Deriso (1982) showed that the discrete fishing mortality rate generated by his delay-difference model at MSY was consistently higher than the discrete natural mortality rate when recruitment was constant, while under several other stock-recruitment assumptions the relationship was reversed. Shepherd (1982) also demonstrated that Rules I and II did not adequately describe the behavior of a particular surplus production model.

Since none of these authors addressed the possibility that other

models might support Rules I and II, it remains to be seen whether these rules are inconsistent only for isolated special cases, or are actually incompatible with a major class of models.

Review of simple dynamic pool models

One place to start in the search for models that might be compatible with Rules I and II is within the family of simple dynamic pool models. As distinguished from surplus production models such as those of Schaefer (1954) and Pella and Tomlinson (1969), dynamic pool models describe stock dynamics in terms of the individual processes of recruitment, growth, and mortality, and incorporate age structure at least implicitly (e.g., Pitcher and Hart 1982). Within the broad class of dynamic pool models, a model will be referred to here as "simple" if it reflects the following assumptions: (A) Cohort dynamics are of continuous-time form, (B) vital rates are constant with respect to time and age, (C) fish mature and recruit to the fishery continuously and at the same invariant ("knife-edge") age, (D) mean body weight-at-age is determined by age alone, (E) the stock (or population) consists of the pool of recruited individuals, (F) maximum age is infinite, (G) the stock is in an equilibrium state determined by the fishing mortality rate, and (H) recruitment is determined by stock biomass alone. Within the framework provided by these assumptions, particular models are distinguished by the forms assigned to the weight-at-age and stock-recruitment functions.

Assumptions (A–C) imply that simple dynamic pool models conform to the following pair of equations:

$$\frac{\partial n(F, a)}{\partial a} = -n(F, a)Z, \tag{1}$$

and

$$n(F, a) = n(F, a_r)\, e^{-Z(a-a_r)}, \tag{2}$$

where a = age, $n(F, a)$ is the stationary population distribution (in numbers) by ages a when the stock is exploited at a fishing mortality rate of F, Z is the instantaneous rate of total mortality (F + M), and a_r is the age of recruitment.

Equation (1) gives the instantaneous rate of change, by age, of the distribution n. When integrated with Z constant (Assumption B), Equation (1) gives Equation (2), numbers as a function of age. Assumption (D) implies that Equation (2) can be cast in terms of biomass by multiplying both sides of the equation by the weight-at-age function $w(a)$:

$$b(F, a) = W(a)\, n(F, a_r)\, e^{-Z(a-a_r)}, \tag{3}$$

where $b(F, a)$ is the stationary population distribution (in biomass) by ages a when the stock is exploited at a fishing mortality rate of F.

Assumptions (B), (C), (E), and (F) imply that total equilibrium stock numbers can be obtained by integrating Equation (2) from $a = a_r$ to $a = \infty$, giving

$$N(F) = \frac{n(F, a_r)}{Z}, \tag{4}$$

where $N(F)$ represents total equilibrium numbers when the stock is exploited at a fishing mortality rate of F.

Likewise, equilibrium stock biomass is obtained by integrating Equation (3) from $a = a_r$ to $a = \infty$:

$$B(F) = n(F, a_r) \int_{a_r}^{\infty} w(a)\, e^{-Z(a-a_r)}\, da. \tag{5}$$

In the case where $a = a_r$, Assumptions (G) and (H) imply that the left-hand side of Equation (3), recruitment biomass, is a deterministic function of equilibrium stock biomass $r(B(F))$:

$$b(F, a_r) = r(B(F)). \tag{6}$$

Average weight of individuals in the stock $W(F)$ can be written

$$W(F) = \frac{\int_{a_r}^{\infty} w(a)\, e^{-Z(a-a_r)}\, da}{\int_{a_r}^{\infty} e^{-Z(a-a_r)}\, da}$$

$$= Z \int_{a_r}^{\infty} w(a)\, e^{-Z(a-a_r)}\, da. \tag{7}$$

Equation (5) can then be rewritten

$$B(F) = \frac{W(F)\, n(F, a_r)}{Z}. \tag{8}$$

For the case of a pristine stock (F = 0), Equations (4) and (8) imply that equilibrium stock size (in terms of

numbers and biomass, respectively) is given by

$$N(0) = \frac{n(0, a_r)}{M}, \quad (9)$$

and

$$B(0) = \frac{W(0)\, n(0, a_r)}{M}. \quad (10)$$

Inconsistency of Rules I and II

The argument of Francis (1974) can be generalized to address more fully the compatibility of Rules I and II. The method to be used is as follows: First, it will be shown that if Rules I and II were to hold simultaneously with the properties of simple dynamic pool models, these rules would imply a particular result. It will then be shown that this result is incompatible with a major subset of the family of simple dynamic pool models, thus proving that Rules I and II are also incompatible with this subset.

Rule II and Equation (10) imply

$$B(F_{MSY}) = \frac{W(0)\, n(0, a_r)}{2M}. \quad (11)$$

Equation (8) implies that $B(F_{MSY})$ must also conform to

$$B(F_{MSY}) = \frac{W(F_{MSY})\, n(F_{MSY}, a_r)}{F_{MSY} + M}. \quad (12)$$

Solving Equations (11) and (12) for F_{MSY} gives

$$F_{MSY} = \left(\frac{2W(F_{MSY})\, n(F_{MSY}, a_r)}{W(0)\, n(0, a_r)} - 1 \right) M. \quad (13)$$

Next, Rule I and Equation (13) imply

$$\frac{n(F_{MSY}, a_r)}{n(0, a_r)} = \frac{W(0)}{W(F_{MSY})}. \quad (14)$$

The left-hand side of Equation (14) can be rewritten

$$\frac{n(F_{MSY}, a_r)}{n(0, a_r)} = \frac{w(a_r)\, n(F_{MSY}, a_r)}{w(a_r)\, n(0, a_r)}$$

$$= \frac{b(F_{MSY}, a_r)}{b(0, a_r)}$$

$$= \frac{r(B(F_{MSY}))}{r(B(0))}. \quad (15)$$

Now let the discussion be restricted to models in which the first derivative of the stock-recruitment relationship is uniformly nonnegative. In such cases, Equation (15) indicates that the left-hand side of Equation (14) is less than or equal to 1 if equilibrium stock biomass decreases as a function of F [i.e., if $B(F_{MSY}) < B(0)$, then $r(B(F_{MSY})) < r(B(0))$]. To examine the conditions under which this occurs, let Equation (8) be rewritten

$$B(F) = \frac{W(F)\, r(B(F))}{w(a_r)\, Z}. \quad (16)$$

Equation (16) can be differentiated as follows:

$$\frac{dB(F)}{dF} = \frac{r(B(F)) \left[Z \left(\frac{dW(F)}{dF} \right) - W(F) \right]}{Z \left[w(a_r)\, Z - W(F) \left(\frac{dr(F(F))}{dB(F)} \right) \right]}. \quad (17)$$

The numerator in Equation (17) is negative whenever $dW(F)/dF < 0$, which is easily shown to be true whenever w(a) is monotone increasing, a characteristic typical of all commonly used growth functions (Schnute 1981).

Thus, it follows that $dB(F)/dF$ will likewise be negative whenever the denominator in Equation (17) is positive; that is, whenever

$$\frac{w(a_r)\, Z}{W(F)} > \frac{dr(F(F))}{dB(F)}. \quad (18)$$

By Equation (16), the left-hand side of (18) can be rewritten as the ratio of r(B(F)) to B(F), giving

$$\frac{r(B(F))}{B(F)} > \frac{dr(B(F))}{dB(F)}. \quad (19)$$

Given that the discussion has been restricted to models with stock-recruitment relationships that are nondecreasing (nonnegative first derivative), a sufficient condition for Equation (19) to hold is for $dr(B(F))/dB(F)$ to be nonincreasing (nonpositive second

derivative). Therefore, for all simple dynamic pool models in which r(B(F)) is nondecreasing and dr(B(F))/dB(F) is nonincreasing, the left-hand side of Equation (14) is less than or equal to 1.0.

Turning to the right-hand side of Equation (14), note that this expression is necessarily greater than 1.0 whenever $dW(F)/dF<0$, a condition which has already been noted to hold whenever w(a) is monotone increasing.

Summarizing the argument, then, it has been shown that Rules I and II cannot hold simultaneously for any simple dynamic pool model in which the first derivative of the stock-recruitment relationship is uniformly nonnegative, the second derivative of the stock-recruitment relationship is uniformly nonpositive, and the first derivative of the weight-at-age relationship is uniformly positive.

Example of a simple dynamic pool model

Growth, biomass, recruitment, and yield

As an alternative to Rules I and II, it is possible to examine the behavior of F_{MSY}/M and $B(F_{MSY})/B(0)$ explicitly for a particular model. The model to be examined here incorporates a linear weight-at-age function (Schnute 1981). Let

$$w(a) = w(a_r)\left(\frac{a-a_0}{a_r-a_0}\right), \tag{20}$$

where a_0 represents the age intercept.

Biomass at age is then

$$b(F,a) = \frac{b(F, a_r)\,(a-a_0)\,e^{-Z(a-a_r)}}{a_r-a_0}, \tag{21}$$

For a given value of $b(F, a_r)$, biomass at age can be integrated from $a=a_r$ to $a=\infty$ to obtain the corresponding equilibrium stock size. Equation (21) can be integrated by parts, giving the following expression for equilibrium stock biomass (Hulme et al. 1947):

$$B(F) = \left(\frac{b(F, a_r)}{a_r-a_0}\right)\int_{a_r}^{\infty}(a-a_0)\,e^{-Z(a-a_r)}\,da$$

$$= \left(\frac{b(F, a_r)}{Z}\right)\left(1+\frac{1}{Z(a_r-a_0)}\right). \tag{22}$$

The stock-recruitment relationship of Cushing (1971) will be used to complete the model, giving recruitment as a power function of stock size:

$$b(F, a_r) = pB(F)^q, \tag{23}$$

where p and q are constants, and $0\leqslant q\leqslant 1$. In the limiting case of $q=0$, recruitment is constant, while in the other limiting case of $q=1$, recruitment is proportional to biomass.

The Cushing stock-recruitment relationship has the advantage of rendering Equation (22) explicitly solvable. Substituting Equation (23) into Equation (22) and rearranging terms gives the following equation for equilibrium stock biomass:

$$B(F) = \left[\frac{p}{Z}\left(1+\frac{1}{Z(a_r-a_0)}\right)\right]^{\frac{1}{1-q}}. \tag{24}$$

Multiplying both sides of Equation (24) by F then gives the equation for yield Y(F) shown below:

$$Y(F) = F\left[\frac{p}{Z}\left(1+\frac{1}{Z(a_r-a_0)}\right)\right]^{\frac{1}{1-q}}. \tag{25}$$

A partitioning of stock production

From this point on, it will prove helpful to make use of a new parameter K″, defined as follows:

$$K'' = \frac{1}{M(a_r-a_0)}. \tag{26}$$

The parameter K″ has a special biological interpretation in the context of the present model. To develop this interpretation, first multiply Equation (22) through by Z, yielding:

$$Z\,B(F) = b(F, a_r)\left(1+\frac{1}{Z(a_r-a_0)}\right). \tag{27}$$

Assuming no immigration or emigration, stock losses due to mortality must equal stock gains due to recruitment and growth at equilibrium (Russell 1931). Since the left-hand side of Equation (27) represents losses due to mortality, the right-hand side must equal the sum of equilibrium recruitment and growth. Therefore, Equation (27) can be rearranged to define equilibrium stock growth G(F) as follows:

$$G(F) = Z\,B(F) - b(F,a_r) = \frac{b(F, a_r)}{Z(a_r-a_0)}. \tag{28}$$

Dividing Equation (28) through by $b(F, a_r)$ gives the ratio between the two components of stock production, i.e., growth and recruitment:

$$\frac{G(F)}{b(F, a_r)} = \frac{1}{Z(a_r - a_0)}. \quad (29)$$

In the case of a pristine stock, Equation (29) reduces to

$$\frac{G(0)}{b(0, a_r)} = \frac{1}{M(a_r - a_0)} = K''. \quad (30)$$

In other words, K'' is simply the pristine ratio of growth to recruitment. At values of $K''>1$ pristine production is dominated by growth, while at $K''=1$ the two components of pristine production are equal, and at values of $K''<1$ pristine production is dominated by recruitment.

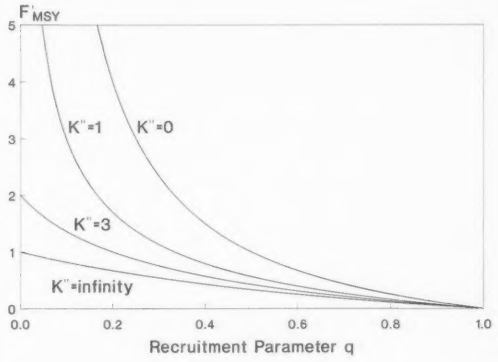

Figure 1

Ratio of F_{MSY} to M. For a given K'' value, the ratio decreases toward zero as q approaches 1.0. Higher K'' values result in lower values of the ratio, reaching a lower limit as K'' approaches infinity.

Fishing mortality at maximum sustainable yield

Differentiating Equation (25) with respect to F and setting the resulting expression equal to zero gives the following equation for F_{MSY}:

$$F_{MSY} = \frac{-\left(\frac{q+1}{a_r - a_0}\right) + M + \sqrt{\left(\frac{q+1}{a_r - a_0}\right)^2 + \left(\frac{(6q-2)M}{a_r - a_0}\right) + M^2}}{2q} - M. \quad (31)$$

Using F' to denote the ratio F/M, Equation (31) can be simplified via Equation (26) to

$$F'_{MSY} = \frac{-(q+1)K'' + 1 + \sqrt{(q+1)^2 K''^2 + (6q-2)K'' + 1}}{2q} - 1. \quad (32)$$

Figure 1 illustrates the behavior of F'_{MSY} as a function of q for four values of K'' (0, 1, 3, and ∞). Note that F'_{MSY} can deviate substantially from the value of 1.0 suggested by Rule I. The locus of parameter values for which Rule I holds under Equation (32) is

$$q = \frac{1}{K''+2}, \quad (33)$$

implying that q must be less than 0.5 in order for Rule I to hold.

When q=1, Equation (32) falls to zero. As q approaches zero, Equation (32) approaches an upper limit F'_{max} defined by

$$F'_{max} = \frac{K''+1}{K''-1}. \quad (34)$$

The limits of Equation (32) as K'' approaches zero and infinity are, respectively,

$$\lim_{K''\to 0} F'_{MSY} = \frac{1-q}{q} \quad (35)$$

and

$$\lim_{K''\to \infty} F'_{MSY} = \frac{1-q}{1+q}. \quad (36)$$

When pristine growth and recruitment are exactly balanced ($K'' = 1$), Equation (32) reduces to

$$F'_{MSY} = \sqrt{\frac{1}{4} + \frac{2}{q}} - \frac{3}{2}. \quad (37)$$

In the case of Equation (34), Rule I is always an underestimate (i.e., F'_{MSY} is always greater than 1.0). In the case of Equation (35), Rule I is an underestimate whenever $q<0.5$ and an overestimate whenever $q>0.5$. In the case of Equation (36), Rule I is always an overestimate, except in the limiting case where $q=0$. In the case of Equation (37), Rule I is an underestimate whenever $q<1/3$ and an overestimate whenever $q>1/3$.

Biomass at MSY relative to pristine biomass

Substituting $M+F_{MSY}$ for Z in Equation (24) gives $B(F_{MSY})$. Likewise, substituting M for Z in Equation (24) gives B(0). Forming a ratio from these two biomasses gives

$$\frac{B(F_{MSY})}{B(0)} = \left(\frac{K'' + F'_{MSY} + 1}{(K''+1)(F'_{MSY}+1)^2} \right)^{\frac{1}{1-q}}, \quad (38)$$

where F'_{MSY} is given by Equation (32).

Equation (38) is illustrated in Figure 2. Note that all of the curves in Figure 2 exhibit the same upper bound (1/e, about 0.37), which is reached in the limit as q approaches 1.0. Thus, Rule II always overestimates Equation (38) by a minimum of about 36%. At values of $q>0.5$, the biomass ratio is always greater than 0.25, but at lower values of q the ratio can be much smaller.

Multiplying Equations (32) and (38) gives the ratio MSY/MB(0), which is plotted in Figure 3. This ratio describes a stock's maximum sustainable fishery-induced losses as a proportion of its pristine losses. Alverson and Pereyra (1969) suggested that the MSY/MB(0) ratio should equal 0.5, a figure obtained by multiplying Rules I and II together. Note that this suggestion errs on the high side whenever K'' exceeds 1.0, as well as whenever q exceeds ~0.23.

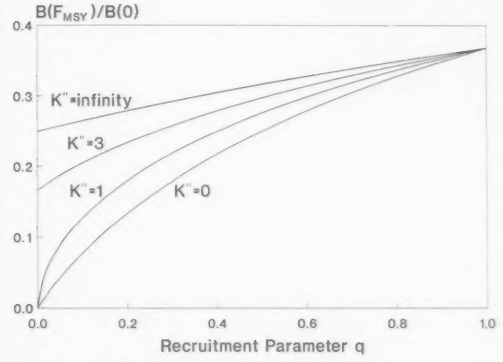

Figure 2

Ratio of $B(F_{MSY})$ to B(0). For any given K'' value, the ratio increases toward a value of 1/e as q approaches 1.0. Higher K'' values result in higher values of the ratio, reaching an upper limit as K'' approaches infinity.

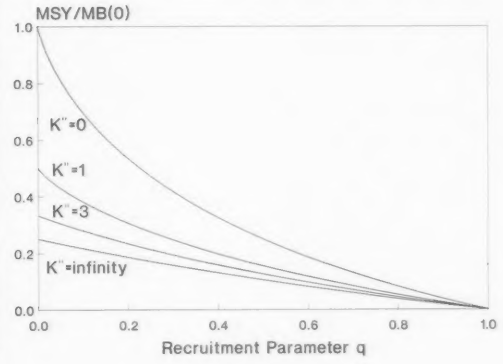

Figure 3

Ratio of MSY to the product of M and B(0). For a given K'' value, the ratio decreases toward a value of zero as q approaches 1.0. Higher K'' values result in lower values of the ratio, reaching a lower limit as K'' approaches infinity.

Applying the model to rock sole

As an illustration of the approach suggested above, the model can be applied to the eastern Bering Sea stock of rock sole *Pleuronectes bilineatus*. This stock is exploited by a multispecies flatfish fishery, and is also the target of an important roe fishery (Walters and Wilderbuer 1988).

The parameters to be estimated are q and K''. The parameter q can be determined from data on stock biomass and recruitment. Trawl survey estimates of rock sole stock biomass are available for the years 1979–88 (Walters and Wilderbuer 1988). In addition, age composition of the stock has been determined for the years 1979–87. In order to obtain an estimate of age composition for 1988, the "iterated age-length key" approach of Kimura and Chikuni (1987) was applied to the 1986 age-length key and the 1988 length-

frequency distribution. Assuming that rock sole recruit at age 3 (Walters and Wilderbuer 1988), these data provide seven years of information on the stock-recruitment relationship. Fitting Eq. (23) to these seven points (assuming lognormal error, Fig. 4) gives $q = 0.235$.

The composite parameter K'' can be estimated from its constituent parameters a_r, a_0, and M (Eq. 26). Walters and Wilderbuer (1988) set $a_r = 3$ and $M = 0.2$. The parameter a_0 can be derived by regressing a line through the mean weights-at-age, as shown in Figure 5 ($R^2 = 0.904$). This gives an a_0 value of 1.475 years, implying a K'' value of 3.279.

With these parameter values, Equation (32) gives $F'_{MSY} = 0.880$, or $F_{MSY} = 0.176$. This estimate of F_{MSY} compares favorably with the value of 0.155 that Walters and Wilderbuer (1988) derived from a surplus production model. It is relatively close to (within 12% of) the value indicated by Rule I.

However, Rule II does not fare so well in this example. Equation (38) estimates the ratio between $B(F_{MSY})$ and $B(0)$ at a value of 0.245, 51% below the value predicted by Rule II.

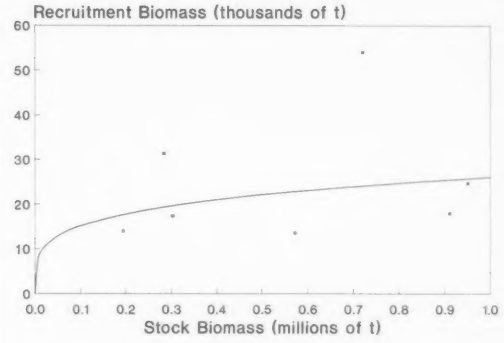

Figure 4

Stock-recruitment data and curve for eastern Bering Sea rock sole *Pleuronectes bilineatus*. Age-3 biomass (lagged 3 yr) is plotted against stock biomass for the years 1979–88.

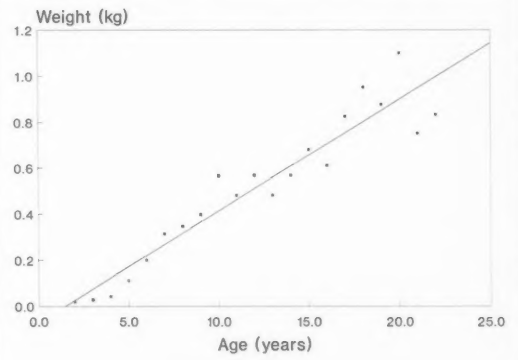

Figure 5

Weight-at-age data and relationship for eastern Bering Sea rock sole *Pleuronectes bilineatus*. Data are from the 1986 trawl survey conducted by the Alaska Fisheries Science Center.

Discussion

The topic of this paper, management advice from a simple dynamic pool model, has been considered from the perspective of how two commonly used rules of thumb compare with simple dynamic pool models in general, and how they compare with one such model in particular.

Choice of functional forms

Within the family of simple dynamic pool models, a particular model is defined by its stock-recruitment and growth functions. As Paulik (1973) and Ricker (1979) state, the choice of functional form for these two processes is largely a matter of convenience. The linear growth and Cushing stock-recruitment functions have been chosen for the proposed model, in part because of the tractability they confer. For example, their use permits explicit specification of F_{MSY} (impossible in other known examples of simple dynamic pool models, except in the special case where $F_{MSY} = F_{max}$). Another advantage is economy of parametrization: only two parameters (K'' and q) are required. The main disadvantage is the possibility that the simplicity of these functional forms might ignore critical behaviors.

The linear growth assumption is probably the more controversial of the two choices. The primary criticism of the linear growth equation is that it implies a constant growth rate, whereas other commonly used functions exhibit decreasing growth rates at upper ages (Beverton and Holt 1957), usually manifested in the form of an upper asymptote. In practice, however, the absence of an asymptote may be inconsequential or even preferable (Knight 1968, Ricker 1979) for two reasons: (1) In exploited populations, individuals may only rarely survive to reach the portion of the growth curve where a marked decrease in growth rate would be most discernible; and (2) in functional forms that incorporate an asymptote, this parameter is often poorly estimated, being highly correlated with at least one other parameter in the equation.

Robustness of the rules of thumb

Neither Rule I nor Rule II is particularly robust when applied to simple dynamic pool models in general or to the model developed here in particular. Rule I can drastically over- or underestimate the true relationship between F_{MSY} and M. When q exceeds 0.5, Rule I consistently overestimates the ratio between F_{MSY} and M, whereas when q is less than 0.5, the ratio can range both well above and well below the value suggested by Rule I.

Although these results do not provide much theoretical support for Rule I, it is still possible that Rule I holds as an empirical generalization (it turned out to be fairly close in the case of eastern Bering Sea rock sole, for example). If Rule I does hold as an empirical generalization, Equation (33) indicates that this implies an inverse relationship between the relative importance of growth in pristine production (K″) and the degree of density-dependence in the stock-recruitment relationship (q). Further work is necessary to see if such an inverse relationship is supported on the basis of life history or other theory.

Rule II consistently overestimates the ratio between $B(F_{MSY})$ and B(0) in the model presented here (Eq. 38, Fig. 2). In the case of eastern Bering Sea rock sole, Rule II was off by 51%. The problem with Rule II stems from the "diminishing returns" nature of the relationship between F and B(F), wherein successive increases in F result in less and less of an impact on biomass. Rule II, on the other hand, was inspired by the Schaefer (1954) model, in which the relationship between F and B(F) is linear (i.e., it exhibits constant returns to scale).

Interestingly, the upper asymptote displayed in Figure 2 corresponds exactly to the asymptote observed in a pair of surplus production models proposed by Pella and Tomlinson (1969, reparametrized by Fletcher 1978) and Fowler (1981), models that are conceptually very different from the one presented here. Mathematically, the isomorphism stems from the fact that all three models involve functions that raise a parameter x to an exponent of the form $1/(1-x)$. The fact that this result can be obtained from both surplus production and dynamic pool models indicates that it may be worthy of further investigation.

Since the rule of thumb setting MSY/MB(0) equal to 0.5 was derived by multiplying Rules I and II, it is affected by the upward bias inherent in Rule II. This is reflected in the eastern Bering Sea rock sole example, where the estimated value for the MSY/MB(0) ratio was only 0.216. It appears that the "MSY/MB(0) rule" can be a good approximation only when Rule I results in a major underestimate, which in the context of the model developed here requires two things: (1) Recruitment must be relatively independent of stock size, and (2) pristine production must be relatively dependent on recruitment (Fig. 3). Another consequence of this relationship is that Rule I can never hold when MSY/MB(0) = 0.5, and vice-versa. This conclusion stands in stark contrast to the traditional view which holds that the MSY/MB(0) rule derives from Rule I. Instead, it seems more likely that the two are mutually exclusive, at least in the context of simple dynamic pool models.

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Abstract. – A simple dynamic pool model is used to examine the problem of stock-recruitment parameter uncertainty from a Bayesian perspective. Probabilities associated with different parameter values are used to weight the losses (i.e., opportunity costs to society) associated with any given fishing mortality rate. By choosing appropriate forms for the loss and probability density functions, the model is shown to result in an analytic solution. Because this solution gives the fishing mortality rate that maximizes the expected value of the logarithm of sustainable yield, it is denoted F_{MELSY}. The solution is a monotone-decreasing function of parameter uncertainty, converging on the fishing mortality rate corresponding to maximum sustainable yield as the degree of uncertainty approaches zero. As an empirical illustration, the model is applied to the eastern Bering Sea stock of rock sole *Pleuronectes bilineatus*.

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A Bayesian approach to management advice when stock-recruitment parameters are uncertain

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Exploiting a stock at the fishing mortality rate (F) associated with maximum sustainable yield (MSY) is a common fishery management strategy. For the most part, three simple propositions are sufficient to justify this strategy: (1) The stock exhibits a sustainable yield determined by the fishing mortality rate, (2) more sustainable yield is always preferable to less, and (3) the parameters underlying the stock's dynamics are known with certainty. However, parameters governing stock dynamics are typically not known with certainty, and in such cases it is possible to demonstrate that the appropriate F value may be less than the value corresponding to MSY (F_{MSY}).

The approach to be used in this demonstration is taken from Bayesian decision theory (e.g., Raiffa 1968, DeGroot 1970). Early applications of Bayesian theory to fisheries problems were presented by Rothschild (1972), Lord (1973, 1976), Walters (1975), and Walters and Hilborn (1976). Of the many more recent applications, those presented by Ludwig and Walters (1982), Clark et al. (1985), and Walters and Ludwig (1987) bear most closely on the present study.

For simplicity, it will be assumed here that stock dynamics are deterministic but governed by parameters which may be imprecisely estimated. This approach is distinct from the more common one of assuming that stock dynamics are the product of a deterministic system (with parameter values given and fixed) modified by a random error term. Important early examples of the latter approach include Ricker (1958), Larkin and Ricker (1964), and Tautz et al. (1969). Ludwig and Walters (1982) and Mangel and Clark (1983) incorporate both approaches in a systematic fashion which makes the distinction especially clear.

The basic model

Thompson (1992) developed a simple dynamic pool model which can be solved explicitly for F_{MSY}. In terms of biomass per recruit, the model is basically that of Hulme et al. (1947); thus, body weight is taken to be a linear function of age, with intercept a_0. The main departure from Hulme et al. is that biomass at recruitment age a_r is taken to be proportional to stock biomass raised to a power q (Cushing 1971). With these specifications, sustainable yield Y(F) can be written

$$Y(F) = F\left[\left(\frac{p}{M}\right)\left(\frac{1+K''+F'}{(1+F')^2}\right)\right]^{\frac{1}{1-q}}, \quad (1)$$

where M is the instantaneous rate of natural mortality, $F' = F/M$, p is the proportionality term in the Cushing stock-recruitment relationship, and $K'' = 1/[M(a_r - a_0)]$ (which can be interpreted in this model as the pristine ratio of growth to recruitment). The

Cushing exponent q is constrained to fall between 0 and 1. In the limiting case of $q=0$, recruitment is constant, while in the other limiting case of $q=1$, recruitment is proportional to biomass.

Differentiating Equation (1) with respect to F and setting the resulting expression equal to zero gives the following equation for F_{MSY}:

$$F'_{MSY} = \frac{-(q+1)K'' + 1 + \sqrt{(q+1)^2K''^2 + (6q-2)K'' + 1}}{2q} - 1, \quad (2)$$

where $F'_{MSY} = F_{MSY}/M$.

A common rule of thumb is that F'_{MSY} should equal 1. The locus of parameter values for which this rule holds precisely is given by

$$K'' = \frac{1}{q} - 2. \quad (3)$$

Analyzing the model in a Bayesian framework

Parameter estimates in any model are by definition associated with some degree of uncertainty. For example, parameters governing the stock-recruitment relationship are particularly difficult to estimate precisely (Larkin 1973, Paulik 1973, Ludwig and Walters 1981, Walters and Ludwig 1981 and 1987, Shepherd 1982, Clark 1985, Clark et al. 1985, Rothschild and Mullen 1985, Shepherd and Cushing 1990). In the presence of such uncertainty, a Bayesian approach would use the probabilities associated with different parameter values to weight the losses (i.e., opportunity costs to society) associated with choosing a particular fishing mortality rate. Following similar studies by Ludwig and Walters (1982), Clark et al. (1985), and Walters and Ludwig (1987), the present analysis will focus on the uncertainty surrounding a single parameter, in this case the stock-recruitment exponent q. This uncertainty takes the form of a probability density function (pdf) P(q) which describes the relative credibility of alternative q values.

To simplify notation, define z(F, q) as the ratio of Y(F) to MSY for an arbitrary value of q drawn from P(q). Then, the "Bayes decision" (DeGroot 1970) is the value of F that minimizes

$$E\{L[z(F, q)]\} = \int_0^1 L[z(F, q)]\, P(q)\, dq, \quad (4)$$

where L[z(F, q)] represents the losses resulting from selection of a particular value of F given a particular value of q, and $E\{L[z(F, q)]\}$ is the expected value of L[z(F, q)] (the "risk," DeGroot 1970). The minimum value of $E\{L[z(F, q)]\}$ is referred to as the "Bayes risk" (DeGroot 1970). The integral is taken over the interval 0 to 1 because the Cushing stock-recruitment relationship constrains q to that range.

The Bayes decision can be derived by differentiating $E\{L[z(F, q)]\}$ with respect to F and solving for the value that sets the derivative equal to zero. The validity of this procedure requires that all parameter values, including those describing P(q), remain constant into the future. The solution corresponding to such an assumption is sometimes known as a "myopic Bayes" solution (Ludwig and Walters 1982, Mangel and Clark 1983, Mangel and Plant 1985, Parma 1990). A more general alternative is to allow for the possibility that parameter estimates will be updated in the future, but this approach is vastly more difficult (Clark et al. 1985, Mangel and Plant 1985, Walters and Ludwig 1987).

Minimizing risk under a logarithmic loss function

Of course, specification of the functions L and P is crucial to this problem. Following Lord (1976) and Ludwig and Walters (1982), one possible choice is to assume that L is a linear function of $z(L(z)=1-z)$. Another common form is the quadratic $L(z)=(1-z)^2$, which has been used in the fisheries literature by Walters (1975), Hightower and Grossman (1987), and Charles (1988). One of the oldest alternatives is the logarithmic loss function, $L(z)=-\ln(z)$, dating back to the work of Bernoulli in 1738 (transl. 1954). Logarithmic loss (or, conversely, utility) seems first to have been used in the fisheries literature by Gleit (1978), followed by Lewis (1981, 1982), Mendelssohn (1982), Opaluch and Bockstael (1984), Ruppert et al. (1984, 1985), Deriso (1985), Walters (1987), Walters and Ludwig (1987), Getz and Haight (1989), Hightower and Lenarz (1989), Hightower (1990), Parma (1990), and Parma and Deriso (1990).

Linear, quadratic, and logarithmic loss functions are compared in Figure 1. As Figure 1 indicates, the logarithmic loss function corresponds to a "preservationist" viewpoint, in which extinction of the stock is absolutely unacceptable (i.e., the loss corresponding to extinction is infinite). Because the logarithmic loss function is clearly identifiable as a risk-averse alternative function (see Discussion), it is a good candidate for illustrating how a Bayesian approach can differ from more traditional approaches which do not incorporate uncertainty in an explicit fashion.

To incorporate the logarithmic loss concept into the model, first note that Equation (1) allows z(F, q) to be written

$$z(F, q) = \frac{Y(F)}{MSY} = \frac{F\left[\left(\frac{p}{M}\right)\left(\frac{1+K''+F'}{(1-F')^2}\right)\right]^{\frac{1}{1-q}}}{F_{MSY}\left[\left(\frac{p}{M}\right)\left(\frac{1+K''+F'_{MSY}}{(1+F'_{MSY})^2}\right)\right]^{\frac{1}{1-q}}} = \frac{F'}{F'_{MSY}}\left[\left(\frac{1+F'_{MSY}}{1+F'}\right)^2\left(\frac{1+K''+F'}{1+K''+F'_{MSY}}\right)\right]^{\frac{1}{1-q}}. \quad (5)$$

For an arbitrary value of q, the (logarithmic) loss associated with a given choice of F is thus

$$L[z(F, q)] = \ln(F'_{MSY}) - \frac{2\ln(1+F'_{MSY}) - \ln(1+K''+F'_{MSY})}{1-q} - \ln(F') + \frac{2\ln(1+F') - \ln(1+K''+F')}{1-q}. \quad (6)$$

Substituting Equation (6) into Equation (4), the risk can be written

$$E\{L[z(F, q)]\} = \int_0^1 P(q)\left(\ln(F'_{MSY}) - \frac{2\ln(1+F'_{MSY}) - \ln(1+K''+F'_{MSY})}{1-q}\right) dq$$

$$- \int_0^1 P(q)\left(\ln(F') - \frac{2\ln(1+F') - \ln(1+K''+F')}{1-q}\right) dq. \quad (7)$$

From Equation (2), it is clear that F'_{MSY} involves only K″ and q. Thus, regardless of the form of P(q), the first integral on the right-hand side of Equation (7) is independent of F. Therefore, the problem of finding the Bayes decision is equivalent to minimizing the second integral on the right-hand side of Equation (7). Remembering that the integral (taken over the interval 0 to 1) of a constant multiplied by P(q) is equal to the constant itself, the following proxy objective function is obtained:

$$E_1\{L[z(F, q)]\} = -\ln(F') + [2\ln(1+F') - \ln(1+K''+F')]\int_0^1 \frac{P(q)}{1-q}\, dq. \quad (8)$$

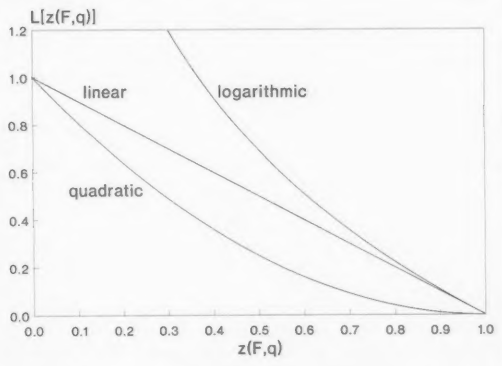

Figure 1
Three possible loss functions. Loss, or relative utility foregone, is plotted against the ratio of Y(F)/MSY for quadratic, linear, and logarithmic loss functions.

Incorporating a beta probability density function

The next step in determining the Bayes decision is to select a form for the pdf P(q). Bayesian decision theory frequently makes use of the beta family of pdfs (e.g., DeGroot 1970, Holloway 1979). The beta distribution would seem to be a natural candidate for P(q), since it constrains q to the necessary (0,1) range. In its standard form, the beta distribution can be written

$$P(q) = \left(\frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\,\Gamma(\beta)}\right) q^{\alpha-1}\,(1-q)^{\beta-1}, \tag{9}$$

where α and β are positive constants and $\Gamma(\cdot)$ is the gamma function, which, except for $\Gamma(1)=1$, can be described in terms of the recursion formula

$$\Gamma(\alpha) = (\alpha-1)\,\Gamma(\alpha-1). \tag{10}$$

By Equations (9) and (10), then, the integral in Equation (8) can be evaluated as follows:

$$\int_0^1 \frac{P(q)}{1-q}\,dq = \left(\frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\,\Gamma(\beta)}\right)\int_0^1 q^{\alpha-1}\,(1-q)^{\beta-2}\,dq = \left(\frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\,\Gamma(\beta)}\right)\left(\frac{\Gamma(\alpha)\,\Gamma(\beta-1)}{\Gamma(\alpha+\beta-1)}\right)$$

$$= \left(\frac{\Gamma(\beta-1)}{\Gamma(\beta)}\right)\left(\frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha+\beta-1)}\right) = \frac{\alpha+\beta-1}{\beta-1}. \tag{11}$$

Substituting Equation (11) into Equation (8) then gives

$$E_1\{L[z(F, q)]\} = -\ln(F') + \frac{[2\ln(1+F') - \ln(1+K''+F')]\,(\alpha+\beta-1)}{\beta-1}. \tag{12}$$

Differentiating Equation (12) with respect to F' and setting the resulting expression equal to zero yields the quadratic expression

$$\alpha F'^2 + [K''(2\alpha+\beta-1) + \alpha - \beta + 1]\,F' - (\beta-1)\,(K''+1) = 0. \tag{13}$$

Before solving Equation (13), it would be helpful to cast the solution in terms of parameters which are more intuitive than α and β, for example the mean and variance of $P(q)$. The beta distribution has mean m and variance v as follows:

$$m = \frac{\alpha}{\alpha+\beta} \qquad \text{and} \qquad v = \frac{\alpha\beta}{(\alpha+\beta)^2\,(\alpha+\beta+1)}. \tag{14) and (15}$$

Conversely, Equations (14) and (15) can be solved simultaneously to describe α and β in terms of m and v:

$$\alpha = \left(\frac{m(1-m)}{v} - 1\right) m \qquad \text{and} \qquad \beta = \left(\frac{m(1-m)}{v} - 1\right)(1-m). \tag{16) and (17}$$

Unlike the normal distribution, the variance of the beta distribution exhibits a maximum possible value for a given mean. Remembering that α and β are constrained to be positive, the maximum possible value of v can be derived from either Equation (16) or Equation (17) by setting the left-hand side equal to 0 and solving for v. This exercise results in a maximum v equal to $m(1-m)$. Thus, α and β can be written in terms of the mean and a scaled variance $v'\left(=\dfrac{v}{m(1-m)}\right)$ as follows:

$$\alpha = \left(\frac{1}{v'} - 1\right) m \qquad \text{and} \qquad \beta = \left(\frac{1}{v'} - 1\right)(1-m). \qquad (18) \text{ and } (19)$$

For a given set of K″, m, and v′ values, Figure 2 shows the risk (depicted by the area under a particular curve) associated with three possible F′ values.

Fishing mortality at maximum expected log-sustainable yield

Substituting Equations (18) and (19) into Equation (13) and solving for F′ gives the value that minimizes risk. Because of the form used for the loss function, this process is equivalent to finding the level of F′ that maximizes the expected value of the logarithm of sustainable yield. It is thus convenient to refer to this value as F'_{MELSY} (for "maximum expected log sustainable yield"), which for this particular model can be written

$$F'_{MELSY} = \frac{[(m+2)\,K''-2]\,v' - (m+1)\,K'' + 1 + \sqrt{k_2\,v'^2 - k_1\,v' + k_0}}{2\,m(1-v')} - 1, \qquad (20)$$

where $k_2 = (m+2)^2\,K''^2 + (12m-8)\,K'' + 4,$
$k_1 = (2m^2+6m+4)\,K''^2 + (18m-8)\,K'' + 4,$ and
$k_0 = (m+1)^2\,K''^2 + (6m-2)\,K'' + 1.$

Figure 3 illustrates how F'_{MELSY} varies with K″, m, and v′. A few special cases are of particular interest. For example, when q is known with certainty, i.e., m = q and v′ = 0, Equation (20) reduces to Equation (2). Equation (2) is thus the "certainty equivalent" solution (Ludwig and Walters 1982). The ratio between F_{MELSY} and F_{MSY} is illustrated in Figure 4. Differences in K″ tend to have less influence on this ratio than differences in either m or v′.

Other important special cases of Equation (20) include the limits as K″ approaches zero and infinity, which are shown respectively below:

$$\lim_{K''\to 0} F'_{MELSY} = \frac{1-m(1-v')-2v'}{m(1-v')} \qquad \text{and} \qquad \lim_{K''\to\infty} F'_{MELSY} = \frac{1-m(1-v')-2v'}{1+m(1-v')-2v'}. \qquad (21) \text{ and } (22)$$

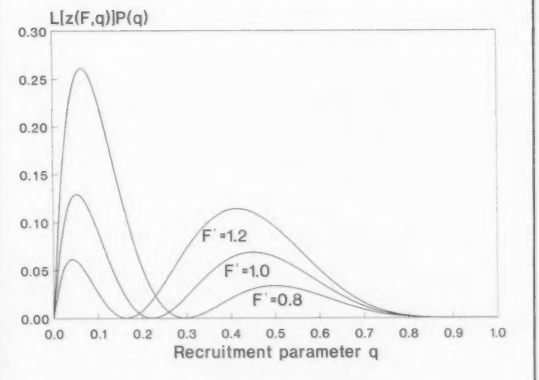

Figure 2
Risk under different F levels. The area under a curve is the risk associated with the F level that defines the particular curve. Parameter values used to generate these curves were K″ = 2.5, m = 0.2, and v′ = 1/11.

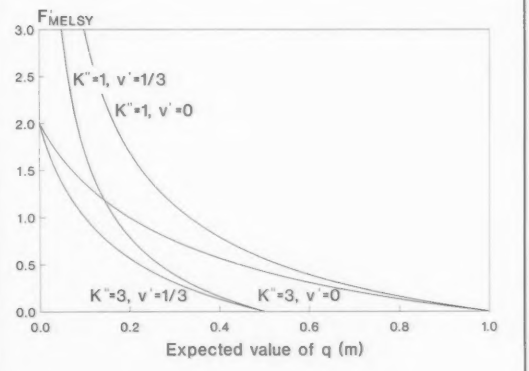

Figure 3
Values of F'_{MELSY} resulting from different combinations of parameter levels. F'_{MELSY} tends to decrease as K″, m, or v′ increases.

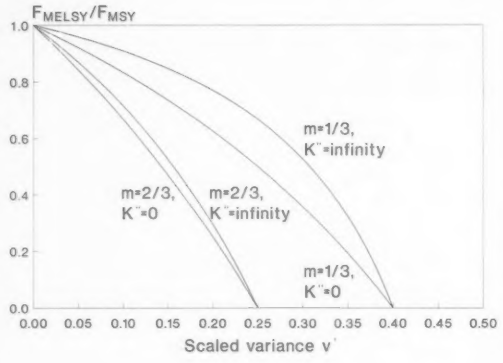

Figure 4

Ratio of F'_{MELSY} to F'_{MSY} under different combinations of parameter levels. The ratio tends to decrease as K″ decreases or as m or v′ increases.

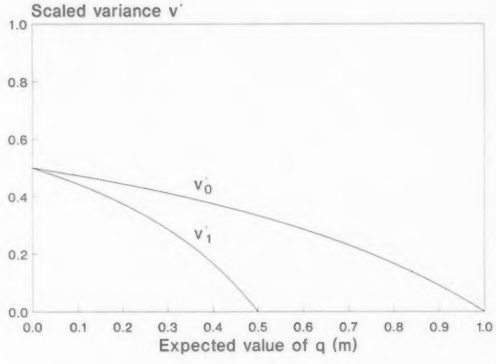

Figure 5

Limiting values of v′. The solid curve shows v'_0, the locus at which $F'_{MELSY} = 0$. The dashed curve shows v'_1, the locus limiting the parameter subspace for which F'_{MELSY} can exceed 1. For (m, v′) combinations below the v'_1 curve, F'_{MELSY} can take any value, depending on K″. For (m, v′) combinations between the two curves, F'_{MELSY} can range between 0 and 1, again depending on K″. For (m, v′) combinations on or above the v'_0 curve, $F'_{MELSY} = 0$.

Equation (20) also implies that F'_{MELSY} falls to zero whenever v′ reaches a critical value v'_0 defined as

$$v'_0 = \frac{1-m}{2-m}. \tag{23}$$

By Equation (19), v'_0 corresponds to a β value of 1. Whenever $\beta \leq 1$, the right-hand tail of the beta distribution fails to reach zero, implying a non-zero probability that q = 1. When q = 1, any positive F value causes the stock to go extinct. Given the preservationist attitude implicit in the logarithmic loss function, any possibility of extinction is unacceptable, so F'_{MELSY} drops to zero in this case. Note that F'_{MELSY} is never positive for values of v′ greater than 0.5.

Just as Equation (2) could be solved to determine the locus of parameter values under which F'_{MSY} takes on the special value of 1 (Eq. 3), Equation (20) can be solved to determine the following locus of parameter values under which $F'_{MELSY} = 1$:

$$K'' = \frac{1-2v'}{m(1-v')} - 2. \tag{24}$$

In the certainty equivalent case, Equation (24) reduces to Equation (3). As K″ approaches zero, Equation (24) defines an upper limit on v′ (v'_1) for the special case where $F'_{MELSY} = 1$:

$$v'_1 = \frac{1-2m}{2-2m}. \tag{25}$$

Under Equation (3), F'_{MSY} could exceed 1 only if q were less than 0.5. While Equation (25) implies essentially the same property (replacing F'_{MSY} with F'_{MELSY} and q with m), it adds a similar restriction on v′, namely that F'_{MELSY} can exceed 1 only if v′ is less than 0.5. [Note that this is a weaker version of the restriction implied by Equation (23). Equations (23) and (25) are compared in Figure 5.]

Biomass at MSY compared with biomass at MELSY

Dividing Equation (1) through by F gives equilibrium stock biomass. By substituting Equations (20) and (2) into this expression and setting q = m, the ratio of stock biomass at MSY to stock biomass at MELSY is given by

$$\frac{B(F_{MSY})}{B(F_{MELSY})} = \left[\left(\frac{F'_{MELSY}+1}{F'_{MSY}+1}\right)^2 \left(\frac{K''+F'_{MSY}+1}{K''+F'_{MELSY}+1}\right)\right]^{\frac{1}{1-m}}, \tag{26}$$

with limits

$$\lim_{K''\to 0}\left(\frac{B(F_{MSY})}{B(F_{MELSY})}\right) = \left(\frac{1-2v'}{1-v'}\right)^{\frac{1}{1-m}} \quad \text{and} \quad \lim_{K''\to\infty}\left(\frac{B(F_{MSY})}{B(F_{MELSY})}\right) = \left(\frac{(1+m)(1-2v')}{(1+m)(1-v') - v'}\right)^{\frac{1}{1-m}}. \qquad (27) \text{ and } (28)$$

Equations (26–28) decline from a value of 1 at $v' = 0$ to a minimum at $v' = v'_0$. The minimum value depends on K'' and m, but is never greater than 1/e.

Estimating the parameters of the beta distribution

To fit the Cushing stock-recruitment curve to a set of n stock-recruitment data points, it seems reasonable to assume the following model:

$$y_i = \rho + qx_i + \varepsilon_i, \qquad (29)$$

where x_i represents the natural logarithm of the ith stock biomass datum, y_i represents the natural logarithm of the ith recruitment datum (lagged according to the age of recruitment), $\rho = \ln(p)$, and ε_i is an independent error term distributed as $N(0,\sigma^2)$.

Press (1989) presented a Bayesian approach to estimating the parameters of the pdf of q using Equation (29) as the underlying model. The following paragraphs summarize this presentation, which begins by rephrasing the problem in the form of Bayes' theorem:

$$h(q,\rho,\sigma \mid \mathbf{x}, \mathbf{y}) \propto \left(\prod_{i=1}^{n} f(y_i \mid x_i,q,\rho,\sigma)\right) g_1(q)\, g_2(\rho)\, g_3(\sigma), \qquad (30)$$

where $\mathbf{x}$ is the vector $(x_1, \ldots, x_n)'$; $\mathbf{y}$ is the vector $(y_1, \ldots, y_n)'$; $h(q,\rho,\sigma \mid \mathbf{x}, \mathbf{y})$ represents the posterior pdf of the parameters q, ρ, and σ; $f(y_i \mid x_i,q,\rho,\sigma)$ represents the conditional pdf of y_i given the observed value of x_i and any particular values of q, ρ, and σ; and $g_j(\cdot)$ represents the prior pdf of the jth parameter.

Given the assumptions implicit in Equation (29), $f(y_i \mid x_i,q,\rho,\sigma)$ can be written

$$f(y_i \mid x_i,q,\rho,\sigma) = \frac{\exp\left(\frac{-(y_i-\rho-qx_i)^2}{2\sigma^2}\right)}{\sqrt{2\pi\sigma^2}}. \qquad (31)$$

A special case of interest is the one in which the $g_j(\cdot)$ are all "vague" (also called noninformative or indifference) priors. These are pdfs which reflect indifference regarding the probability of alternative parameter values. Press (1989) treated $g_1(q)$ and $g_2(\rho)$ as constants, implying that all values on the real line are equally likely in the prior distribution. Since σ is constrained to be positive, however, Press set $g_3(\sigma) = 1/\sigma$, reflecting a uniform prior distribution for $\ln(\sigma)$.

Using Equation (31) and the priors specified by Press (1989), Eq. (30) gives a straightforward solution. The classical least-squares estimates of q and ρ ($\hat{q}$ and $\hat{\rho}$, respectively) obtain as the maximum-likelihood estimates. In their posterior pdf, q and ρ jointly follow a bivariate Student's t distribution, so that marginally the posterior pdf of q, $h_1(q \mid \mathbf{x}, \mathbf{y})$, follows a univariate 3-parameter t distribution with $n-2$ degrees of freedom:

$$h_i(q \mid \mathbf{x},\mathbf{y}) = \frac{\Gamma\left(\frac{n-1}{2}\right)}{\Gamma\left(\frac{n-2}{2}\right)\sqrt{\pi(n-2)\, s_q^2}\left(1 + \frac{(q-\hat{q})^2}{(n-2)\, s_q^2}\right)^{n-1}}, \qquad (32)$$

where s_q^2 is the estimated variance of $\hat{q}$ given by

$$s_q^2 = \frac{\sum_{i=1}^{n} (y_i - \hat{\rho} - \hat{q}x_i)^2}{(n-2)\sum_{i=1}^{n} (x_i - \bar{x})^2}. \quad (33)$$

For the present application, the solution given by Press (1989) needs to be modified in only one respect. His suggested form for $g_1(q)$ implies a uniform distribution over the entire real line, whereas here P(q) has been specified *a priori* to be zero for all values less than 0 or greater than 1. Given Equations (30) and (31), this implies that the suggested uniform shape for $g_1(q)$ should be truncated outside the range 0 to 1. This in turn implies that $h_1(q \mid \mathbf{x},\mathbf{y})$ should also be truncated outside the range 0 to 1 (and rescaled appropriately).

Strictly speaking, then, P(q) follows a truncated t distribution in this approach, rather than the hypothesized beta. However, a beta distribution can be made to approximate the truncated t by solving for m and v as follows:

$$m = \frac{\int_0^1 q\, h_1(q \mid \mathbf{x},\mathbf{y})\, dq}{\int_0^1 h_1(q \mid \mathbf{x},\mathbf{y})\, dq} \quad (34)$$

and

$$v = \frac{\int_0^1 (q-m)^2\, h_1(q \mid \mathbf{x},\mathbf{y})\, dq}{\int_0^1 h_1(q \mid \mathbf{x},\mathbf{y})\, dq}. \quad (35)$$

Applying the model to rock sole

As an illustration of the approach suggested above, the model can be applied to the eastern Bering Sea stock of rock sole *Pleuronectes bilineatus*. This stock is exploited by a multispecies flatfish fishery, and is also the target of an important roe fishery (Walters and Wilderbuer 1988).

The parameters to be estimated are K″, m, and v′. Thompson (1992) estimated K″ for this stock at a value of 3.279, and described a set of stock and recruitment data ($n=7$) which can be used to estimate m and v′. Fitting Equation (29) to these data gives $\hat{q}=0.235$ and $s_q^2=0.114$ (Fig. 6). Substituting these parameters into Equations (34) and (35) gives $m=0.369$ and $v=0.057$, with $v'=0.243$. The relationship between the truncated t distribution defined by these values and the beta approximation is shown in Figure 7 ($R^2=0.97$).

With parameter values $K''=3.279$, $m=0.369$, and $v'=0.243$, Equation (20) gives $F'_{MELSY}=0.365$. Multiplying through by M (set at 0.2 by Walters and Wilderbuer 1988) gives $F'_{MELSY}=0.073$. Substituting m for q in Equation (2) yields $F'_{MSY}=0.607$, or $F_{MSY}=0.121$. This value of F_{MSY} differs somewhat from the value of 0.176 given by Thompson (1992), which was based on the least-squares estimate of q ($\hat{q}$) instead of the

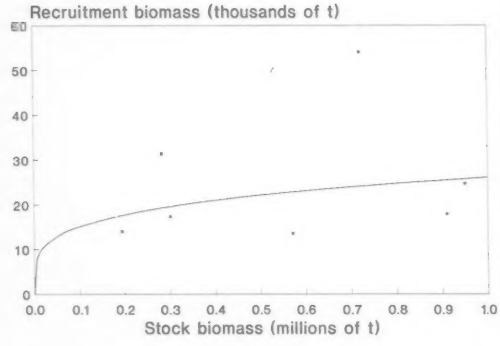

Figure 6

Stock-recruitment data and curve for eastern Bering Sea rock sole *Pleuronectes bilineatus*. Age-3 biomass (lagged 3 yr) is plotted against stock biomass for the years 1979–88. The curve is the least-squares fit.

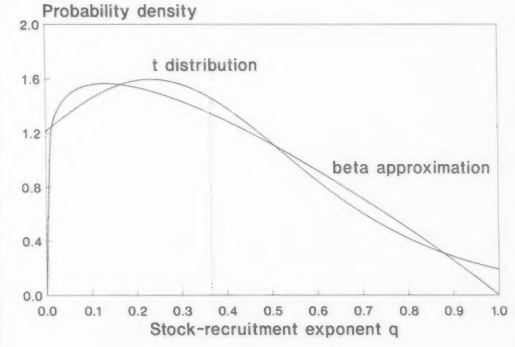

Figure 7

Comparison of truncated t and beta pdfs for the stock-recruitment exponent q in the eastern Bering Sea rock sole *Pleuronectes bilineatus* example.

Bayesian estimate (m). These two F_{MSY} values bracket the value of 0.155 which Walters and Wilderbuer (1988) derived from a surplus production model. Regardless of which F_{MSY} value is chosen, however, it exceeds F_{MELSY} by a significant amount.

Discussion

Evaluation of assumptions

The approach described here consists of three main components: the basic model represented by Equation (1), the logarithmic loss function, and the beta form for P(q). These components were chosen in part because they are tractable, making possible the analytic solution for F'_{MELSY} given by Equation (20). In addition, each has some degree of theoretical support, as described below.

The basic model The basic model was evaluated by Thompson (1992). In brief, the model includes terms for all of the requisite features of dynamic pool models (recruitment, growth, natural mortality, fishing mortality). The distinguishing features of the model (linear growth and a Cushing stock-recruitment relationship) satisfy the principal theoretical requirements for growth and stock-recruitment functions given by Schnute (1981) and Ricker (1975), respectively. Although the basic model is a simple one, it approximates more complicated models fairly well under a wide range of parameter values.

Logarithmic loss function The logarithmic loss function may require a bit more discussion. As mentioned earlier, this loss function is only one of several possibilities, two of the other most-common being the linear and quadratic forms. The principal argument against the linear loss function is that it implies strict risk neutrality, whereas most individuals tend to be at least somewhat risk-averse. Thus, if fishery managers tend to be risk-averse, a linear loss function would be inappropriate, except over a narrow range of yield values.

In contrast, the quadratic loss function implies a degree of risk aversion. In addition, the quadratic form has properties which prove convenient for a number of statistical applications. However, it has also been the subject of substantial criticism (Pratt 1964, Samuelson 1967, Box and Tiao 1973). Although the quadratic loss function does fall into the "risk-averse" category, this functional form manifests its risk aversion somewhat perversely by exhibiting increasing absolute risk aversion (Pratt 1964). In other words, a fishery manager using a quadratic loss function would be less willing to take risks as yields became higher.

The logarithmic loss function is another risk-averse alternative. It can be described as a special case of the isoelastic marginal loss function defined by $L(z)=(1-z^{\phi})/\phi$, where $\phi>0$ (the logarithmic case being obtained in the limit as ϕ approaches zero). Unlike the quadratic loss function, isoelastic marginal loss functions exhibit decreasing absolute risk aversion (Pratt 1964). Isoelastic marginal loss functions also display the convenient property of constant *relative* risk aversion R(z), defined as $-zL''(z)/L'(z)$ (Pratt 1964). Specifically, $R(z)=1-\phi$ for the isoelastic marginal loss family. The logarithmic case, where $R(z)=1$, thus represents a clear risk-averse alternative to the risk-neutral linear loss function, where $\phi=1$ and $R(z)=0$.

The fact that the logarithmic loss function tends toward negative infinity as the resource approaches extinction may be viewed as problematic by some. On the other hand, Smith (1985) views this behavior as a requisite characteristic for any loss function to be used in the context of renewable resources, arguing that it "introduces a useful conservation motive into the decision making process." Opaluch and Bockstael (1984) go even further, stating, "It is well known that the log function exhibits the best properties of the simple functional forms. . . ."

Beta probability density function The principal justification for using the beta pdf to describe P(q) is that the beta is a natural choice for the pdf of any continuous variable which is constrained to fall within the 0 to 1 range. The fact that it allows for an explicit solution to Equation (7) is another argument in its favor.

Unfortunately, the method presented here for estimating the parameters of P(q) is based on a model (Press 1989) which yields a truncated t distribution, not a beta distribution. If this model is accepted as a true description of reality, then the beta form for P(q) is only an approximation. Of course, most functional forms used in modeling are only approximations, so the question is whether the advantages of increased tractability provided by the beta distribution outweigh any attendant losses of accuracy. Holloway (1979) argues in the affirmative after noting the difficulty of identifying natural processes which yield the beta distribution as a formal result.

In general, the effectiveness of Bayes decisions is relatively insensitive to small changes in the assumed pdf (DeGroot 1970). This being the case, the question really is whether the difference between the truncated t distribution and the beta approximation is typically small. To assess the magnitude of this difference, the goodness-of-fit between the truncated t and beta distributions was examined for a wide range of n, $\hat{q}$, and s_q^2 values (Fig. 8). Note that $R^2>0.95$ for a wide range of parameter values, indicating that the loss of

accuracy resulting from the beta approximation is often small.

Another fact to keep in mind is that the model presented by Press (1989) is only one possibility. Despite the pessimism conveyed by Holloway (1979), it is conceivable that other models could yield the beta distribution as an exact result.

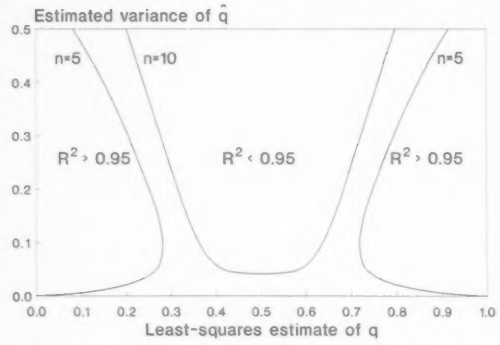

Figure 8

Loci of parameter values under which a beta approximation to the truncated t distribution gives an R^2 value of 0.95. R^2 was calculated by comparing the two distributions at q values of 0.01, 0.02, . . . , 0.99. For $n = 5$, parameter combinations lying to the interior of the two curves correspond to R^2 values <0.95. For $n = 10$, R^2 values <0.95 correspond to parameter combinations lying above the curve.

Comparison with previous studies

Of the many previous applications of Bayesian decision theory to fisheries, the studies by Ludwig and Walters (1982), Clark et al. (1985), and Walters and Ludwig (1987) are most closely related to the present work. The various features of the four approaches are outlined in Table 1. The three previous studies exhibit certain common features which distinguish them from the present study, namely: (1) use of a discrete time scale; (2) inclusion of an explicit adaptive management strategy; (3) inclusion of environmental stochasticity as well as parameter uncertainty; (4) inclusion of a positive discount rate in the objective function; (5) assumption of a normal form for the pdf of the uncertain parameter; and (6) inability to derive an exact analytic solution, even in the myopic case (except for one special instance considered by Clark et al.). The present study is also the only one of the group which includes both a biomass-based model and a risk-averse loss function.

Ludwig and Walters (1982) found that the deterministic optimum escapement level can be less than half the value of the Bayesian solution. Although the continuous form of the model used in the present study makes it difficult to talk about escapement per se, equilibrium stock size might serve as a suitable proxy

Table 1

Comparison of four studies describing Bayesian approaches to fishery management.

Feature	Ludwig and Walters (1982)	Clark et al. (1985)	Walters and Ludwig (1987)	This study
Time scale	discrete	discrete	discrete	continuous
Yield metric	numbers	biomass	numbers	biomass
Adaptive strategy included	yes	yes	yes	no
Age structure included	no (discrete generations)	yes	no (discrete generations)	yes
Discounting included	yes	yes	yes	no
Harvesting costs included	no	yes	no	no
Stochasticity included	yes	yes	yes	no
Loss function	linear	linear	logarithmic	logarithmic
Growth function	none	isometric von Bertalanffy	none	linear
Stock-recruitment function	Ricker (1954)	a) Cushing b) stock-independent c) linear-threshold	Cushing	Cushing
Uncertain parameter	Ricker exponent	a) ln(Cushing multiplier) b) mean ln(recruitment) c) mean ln(recruitment)[1]	Cushing exponent (q)	q
Pdf	normal	normal	normal	beta
Analytic solution obtained	no	case (b) (myopic only)	approximate[2] (myopic only)	yes

[1] Only recruitment data from stock sizes above the threshold were used to calculate the mean.
[2] Approximate solution valid only for pdfs with variance <0.01.

for comparison with the results of Ludwig and Walters. As Equations (26–28) indicate, a variety of parameter combinations allow for $B(F_{MSY})$ to be less than half of $B(F_{MELSY})$. Since the results presented by Ludwig and Walters (1982) were derived from a numbers-based model, Equation (27) is particularly relevant. Under this equation, a v' value greater than 1/3 is sufficient to guarantee that the stock size at MSY will be less than half the stock size at MELSY, regardless of the value of m. At values of $m>0.5$, a v' value of 0.227 is sufficient.

Clark et al. (1985) found that the relationship between the myopic Bayes and certainty-equivalent solutions depended on the model used. In the special case where recruitment is independent of stock size, for example, they found that the myopic Bayes solution always exceeded the certainty equivalent solution. For the same model, the authors also found that the myopic Bayes solution always increased with the level of uncertainty. These results are precisely the opposite of those obtained in the present study, where F_{MELSY} is always less than F_{MSY} and decreases monotonically with v'. In their "full cohort model" with a stock-recruitment relationship, however, Clark et al. (1985) obtained results similar to those of the present study. In one example, the myopic Bayes solution prescribed a 30–50% reduction in F relative to the certainty-equivalent solution. Using yet another model, Walters and Ludwig (1987) also found that the myopic Bayes solution was a monotone-decreasing function of uncertainty.

Conclusion

This paper describes an approach for treating the problem of parameter uncertainty in a systematic fashion. Although fisheries are often managed as though stock parameters are known with certainty, it would be preferable to develop a management approach more consistent with the fact that such certainty is the exception rather than the rule. Such an approach was developed here in the context of Bayesian decision theory. When applied to the particular model presented, this approach indicates that the optimal fishing mortality rate F_{MELSY} (Eq. 20) is always less than F_{MSY} (Eq. 2) except in the limiting case where q is known with certainty (Fig. 4).

This result provides formal support for the intuitive conclusion (e.g., Kimura 1988) that fishing mortality should be strongly constrained when the stock-recruitment relationship is uncertain. Similarly, Equation (25) indicates that if recruitment is highly dependent on stock size (specifically, if m exceeds 0.5), F_{MELSY} will always be less than the natural mortality rate.

The rock sole example illustrates the basic conservatism of the F_{MELSY} approach. In this example, F_{MELSY} was less than F_{MSY} by about 40%. Given that neither the F_{MSY} value (0.121) nor the fit from the stock-recruitment regression (Fig. 6) was atypical of groundfish stocks, the ratio between F_{MELSY} and F_{MSY} in this example provides a practical illustration of the extent to which an explicit accounting for uncertainty can influence management strategy. The magnitude of the effort reduction prescribed in this example is similar to results described by Ludwig and Walters (1982) and Clark et al. (1985). The confirmatory nature of these studies may suggest that the conventional wisdom regarding optimal exploitation rates should be reexamined. At the very least, the F_{MELSY} approach provides a low-end estimate of the maximum acceptable harvest rate and a warning against taking F_{MSY} estimates too seriously.

A great deal of the conservatism resulting from the F_{MELSY} approach as developed here stems from the assumption that all values of q are logically possible, despite the fact that a q value of 1 results in extinction under any level of fishing. One alternative might be to examine q in the context of life-history theory, to determine if it is possible to justify some other upper limit on the logically permissible range. A related alternative would be to use a nonuniform prior in estimating $P(q)$. The assumption of a uniform prior may be overly pessimistic, since fishery biologists often have an intuitive feel for stock-recruitment parameters, even in the absence of data for a particular stock. Such information could be used to define an alternate prior pdf. Another possibility would be to establish an empirical prior based on the results of other stock-recruitment studies, but this would likely require a fairly elaborate weighting scheme so that stock-recruitment parameters from the most dissimilar stocks or environments would have the least influence on the form of the resulting pdf.

An additional factor which may add to the conservatism of the F_{MELSY} strategy as developed here is the use of the myopic Bayes solution rather than an actively adaptive solution. An actively adaptive solution would attempt to anticipate and make use of changes in available information resulting from alternative management actions (e.g., Walters and Hilborn 1976, Smith and Walters 1981, Ludwig and Walters 1982, Ludwig and Hilborn 1983, Clark et al. 1985, Walters 1986, Milliman et al. 1987, Walters and Ludwig 1987, Parma 1990, Parma and Deriso 1990). However, myopic Bayes (or similar) solutions often perform nearly as well as their actively adaptive counterparts (Mendelssohn 1980, Walters and Ludwig 1987, Parma 1990, Parma and Deriso 1990), and if the myopic Bayes solution is reestimated each year, the result is a

passively adaptive strategy which is asymptotically optimal over time (Walters 1987). Most important for the purposes of the present study, though, is the fact that the myopic Bayes solution is computationally much simpler than the actively adaptive solution.

In conclusion, it should be stressed that while the approach suggested here was developed in the context of a particular model and particular loss and probability density functions, this development was meant primarily to illustrate the approach, not to limit it. More sophisticated applications—utilizing alternative assumptions, functional forms, and solution techniques—are certainly to be encouraged. In particular, future research might incorporate recruitment stochasticity, positive discount and cost rates, additional objective function components (e.g., yield variability), and uncertainty in other parameters and variables (e.g., the natural mortality rate, growth rate, and stock size).

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Eastern Pacific species of the genus *Umbrina* (Pisces: Sciaenidae) with a description of a new species

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Abstract.–The only cosmopolitan sciaenid genus, *Umbrina*, is represented in the eastern Pacific Ocean by eight species: *U. analis*, *U. bussingi*, *U. dorsalis*, *U. galapagorum*, *U. reedi*, *U. roncador*, *U. wintersteeni* n. sp., and *U. xanti*. *Umbrina analis* is removed from the synonymy of *U. xanti*. Lectotypes are designated for *U. dorsalis*, *U. galapagorum* and *U. xanti*. *Umbrina wintersteeni*, which usually occurs in shallow, protected waters of the southern Gulf of California and the west coast of southern Baja California Sur, apparently is morphologically intermediate between two major groups of eastern Pacific species. Distinguishing characters of *U. wintersteeni* include peritoneum and inside gill cover with little or no pigment; barbel relatively short and stout; anal fin with six soft rays; anal fin darkly pigmented to dusky; pelvic fins usually dusky; second anal spine of moderate length.

Of the more than 70 genera in the percoid family Sciaenidae, only *Umbrina* has a worldwide distribution (Chao 1986a). The approximately 15 species that constitute *Umbrina* occur in tropical to temperate waters over the continental shelf to the upper slope. In the New World, *Umbrina* comprises four species in the Atlantic (Gilbert 1966, Miller 1971) and eight in the Pacific (this study). Most eastern Pacific species are collected with beach seines over sand or sand-mud bottoms, along open coasts or in bays, and probably support artisanal or sportfisheries wherever they are found. In southern California the yellowfin croaker *U. roncador* and spotfin croaker *Roncador stearnsii*) together make up about 10 percent of the surf fisherman's catch (Frey 1971).

No review of the eastern Pacific species of *Umbrina* has been published, although McPhail (1958) wrote extensive keys to all known eastern Pacific sciaenids, and Lopez S. (1980) described a new species of *Umbrina* from this area. The purposes of this paper are to review the eastern Pacific species of *Umbrina*, provide a key and characters useful in their identification, and describe a new species.

Materials and methods

Counts and measurements generally follow those of Hubbs and Lagler (1958). Gill raker counts include rudiments. Unless otherwise stated, standard length (SL) is used throughout. Vertebral and procurrent caudal ray counts were made from radiographs. A short, stout barbel is defined as one whose length roughly equals its width at midlength (seen in side view); an elongate barbel is at least twice as long as wide. Mean percentages of certain morphometrics used in species diagnoses were calculated usually from 30 specimens, occasionally ~20 (when available), selected from the entire size range of the species. Standard errors associated with these means were calculated strictly to show relative variation for a particular proportion and were always 0.6% (once) or less. All pigmentation notes were made from alcohol-preserved specimens. Institutional abbreviations follow Leviton et al. (1985). There have been many instances where eastern Pacific species have been ascribed to *Umbrina* (e.g., *U. panamensis* = *Menticirrhus panamensis*; *U. imberbis* = *Sciaena*, probably *callaensis*), and these are beyond the scope of this paper. Type material

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of all synonyms listed in the species accounts was examined by the authors and/or C.L. Hubbs (deceased).

Systematics

Genus *Umbrina* Cuvier

Synonymy

Umbrina Cuvier 1816:297 (type species *Sciaena cirrosa* Linnaeus, by monotypy, see Opinion 988, Bull. Zool. Nom. (1972):123).

Attilus Gistel 1848:109 (type species *Sciaena cirrosa* Linnaeus, by monotypy).

Asperina Ostroumoff 1896:30 (type species *A. improviso* (= *U. cirrosa*) Ostroumoff, by monotypy).

Diagnosis Deep-bodied to moderately elongate, compressed sciaenid fishes with a single mental barbel, usually with an apical pore; swim bladder single-chambered, usually carrot-shaped, with no diverticula, located entirely abdominally; preopercular margin with bony serrations; two anal spines, the second long and thick.

Description As in Gilbert (1966), Trewavas (1977), and Chao (1978, 1986a,b), with some additions: back slightly arched; ventral profile nearly straight; head oblong; snout thick and protuberant with 5–7 rostral and 5 marginal pores; chin with two pairs of lateral pores surrounding the short barbel; mouth small, inferior, horizontal or nearly so; teeth small, villiform, set in bands in both jaws, outer row of teeth in upper jaw may be slightly enlarged; sagitta (largest otolith) thick, oval, with smooth inner surface and crested or nodular outer surface; cauda of sulcus bent sharply and not reaching ventral edge of sagitta, ostium reaching anterior edge; gill rakers short; caudal fin truncate to slightly emarginate or pointed; scales ctenoid; vertebrae 10–11 + 14–16 = 25–26; dorsal fin rays IX–X + I, 21–33; anal rays II, 5–10; pectoral rays 14–20; overall background coloration white to silver or yellow to brown; usually with dark-brown stripes: oblique dorsolaterally, more longitudinal midlaterally and on peduncle area, becoming faint or absent ventrally, usually faint or absent on head.

Relationships The genera *Sciaena* and *Umbrina* are the only representatives of the tribe Sciaenini (Chao 1986a). Characters of the swim bladder are the most important factors in assessing the phylogenetic relationships among suprageneric groups of sciaenids and the single-chambered swim bladder, lacking appendages, characteristic of the sciaenines, is the most primitive (plesiomorphic) form (Chao 1986a). The genus *Sciaena* (species have no barbels) is a polyphyletic assemblage containing numerous species and is in need of revision (Chao and Miller 1975, Chao 1986a). Although apparently monophyletic, we presently can only define *Umbrina* with synplesiomorphies or homoplastic apomorphies (e.g., pored mental barbel) (L.N. Chao, Bio-Amazonica Conserv. Int., Brazil, pers. commun., Sept. 1991).

Key to the eastern Pacific species of *Umbrina*

1A Inside gill cover dark to black, particularly in area of pseudobranch 2
1B Inside gill cover pale or lightly punctate 4

2A Dorsal fin with 21–23 soft rays; no stripes on body ..... ***U. bussingi***
2B Dorsal fin usually with 26–30 soft rays; dark to dusky horizontal or oblique stripes on body 3

3A Anal fin normally with 7 soft rays; peritoneum dark ..... ***U. roncador***
3B Anal fin normally with 6 soft rays; peritoneum light ventrally (may be dark dorsally) ..... ***U. xanti***

4A Anal fin with 9(8) soft rays; dorsal fin with IX+I spines ..... ***U. reedi***
4B Anal fin with 6–7(8) soft rays; dorsal fin with X+I spines 5

5A Dorsal fin usually with 30–33 soft rays; snout length less than eye diameter ..... ***U. dorsalis***
5B Dorsal fin usually with 24–29 soft rays; snout length greater than eye diameter (adults) 6

6A Body stripes distinct; pectoral fin rays 17 or fewer; dorsal fin soft rays 27 or fewer 7
6B Body stripes indistinct or lacking; pectoral fin rays usually 18 or more; dorsal fin rays 27 or more ..... ***U. galapagorum***

7A Second anal spine ~1.5 in head; pelvic fins with little or no pigment ..... ***U. analis***
7B Second anal spine ~2.0 in head; pelvic fins usually dusky to dark ..... ***U. wintersteeni***

Umbrina bussingi Lopez S.

Figure 1

Synonymy

Umbrina bussingi Lopez S. 1980:203–208 (original description: holotype LACM 38715-1; Costa Rica).

Diagnosis A small species of *Umbrina* (max. length 252 mm) characterized by the following combination of characters: inside gill cover dark to black; no dark-brown stripes; caudal fin pointed; barbel compressed,

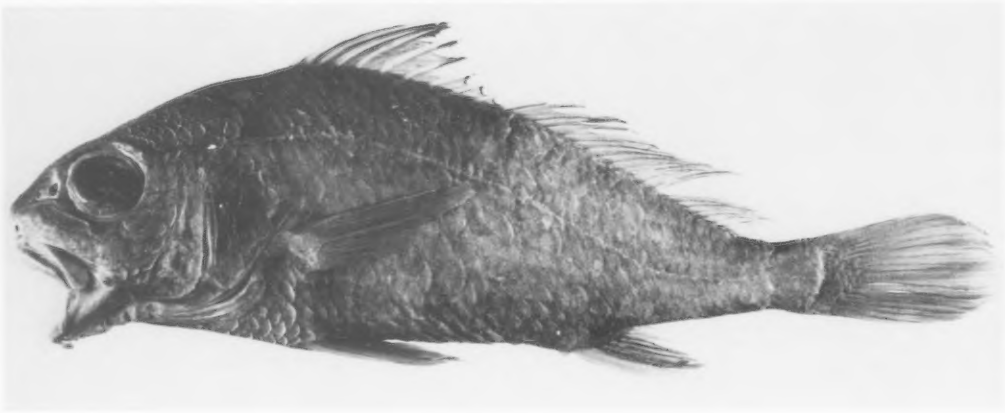

Figure 1
Umbrina bussingi, 230 mm SL, LACM 9099-28.

with anterior, slit-like (vertical) pore (large adults); peritoneum dark to dusky ventrally and laterally, lighter dorsally; soft dorsal fin rays 21–23; soft anal rays 7; pectoral rays usually 18–19; procurrent caudal rays 7–8 + 7–8(9); dorsal spines X + I; gill rakers usually 19–20; vertebrae 10 + 15; length of second anal spine, $\bar{x}$ 17% SL; body depth, $\bar{x}$ 32% SL; eye length, $\bar{x}$ 9% SL; upper-jaw length, $\bar{x}$ 13% SL; pectoral fin length, $\bar{x}$ 26% SL.

Description Counts and measurements are given in Tables 1–6. Soft dorsal and anal fin rays as in Diagnosis. Pectoral rays 17–19; gill rakers 17–22; barbel not fully developed (usually bulbous) on specimens ≥154 mm; pigment inside operculum appears externally as large, dark spot; no dark-brown stripes at any size; background color uniformly light- (in young, to ~155 mm) to medium-brown; second anal spine relatively long and thick; body fairly deep; eye large, relatively smaller in larger specimens, but length always greater than snout length; head and upper jaw relatively long; pectoral fins extremely long, proportionately shorter at larger sizes; lateral line scales 47–49, $\bar{x}$ 47.95, SE 0.18; spinous dorsal fin dark to dusky, lighter in smaller specimens; soft dorsal, pelvic, and caudal fins light to dusky, becoming darker with increasing size, most pigment on pelvic and caudal fins appearing on distal two-thirds; pectoral fins essentially unpigmented; anterior, proximal portion of anal fin darkly pigmented at most sizes, dark pigment on most of fin at larger sizes.

Distribution Southern Gulf of California, south of Los Frailes to Golfo de Chiriqui, Panama (Fig. 2). A relatively deep-living species, taken in depths of 32 m to >183 m (Lopez S. 1980).

Umbrina roncador Jordan and Gilbert
Figure 3

Synonymy
Umbrina roncador Jordan and Gilbert 1882:277–278 (original description: holotype USNM 29371, Bahia Pequeña, Baja California Sur).

Sciaena thompsoni Hubbs 1921:1–3 + pl. (original description: holotype UMMZ 55053, Santa Catalina I., CA).

Diagnosis An intermediate-sized species of *Umbrina* (reported to ~381 mm) characterized by the following: inside gill cover dark to black, particularly in area of pseudobranch; peritoneum usually dark; soft dorsal fin rays usually 26–29; soft anal rays usually 7; pectoral rays usually 17–18; procurrent caudal rays usually 9–10 + 8–9; dorsal spines X + I; gill rakers usually 18–20; vertebrae 10 + 15; barbel relatively elongate, slender, more robust at sizes greater than ~200 mm; length of second anal spine, $\bar{x}$ 12% SL; body depth, $\bar{x}$ 29%; eye length, $\bar{x}$ 6%; upper jaw length, $\bar{x}$ 11%; pectoral fin length, $\bar{x}$ 17%.

Description Counts and measurements are given in Tables 1–6. Soft rays of second dorsal fin 24–31; soft anal rays 6–7; pectoral rays 15–20; gill rakers 15–22; snout length greater than eye diameter (adults); pigment inside operculum usually appears externally as large, dark spot, dark pigment around pseudobranch

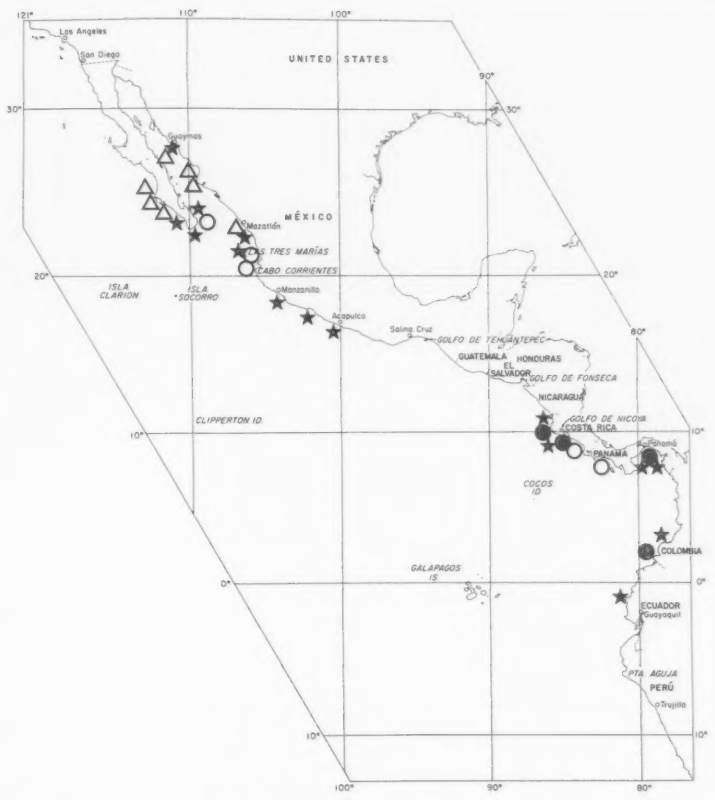

Figure 2
Geographic distribution of *Umbrina bussingi* (○), *U. dorsalis* (★), *U. analis* (●), and *U. wintersteeni* n. sp. (△).

usually present by 50–65 mm; barbel fully developed by ~70 mm, indistinguishable or flat at sizes <30 mm, bulbous between ~30 and 70 mm; lateral line scales 49–54, $\bar{x}$ 50.85, SE 0.04; virtually all brown stripes present by 70 mm; 5–8 dark, vertical bars occasionally on specimens 25–180 mm, usually faint when >80 mm; dorsal fin dusky at most sizes; pectoral, pelvic, anal, and caudal fins usually with little or no pigment, caudal occasionally dusky.

Distribution Point Conception to Bahia Magdalena and disjunctly in the northern Gulf of California, north of 27°N (Fig. 4). Taken in bays and the surf zone to ~45 m (Miller and Lea 1972).

Umbrina xanti Gill
Figure 5

Synonymy

Umbrina xanti Gill 1862:257–258 (original description: syntypes USNM 7156, USNM 2996, USNM 3693, USNM 3694, Cabo San Lucas, Baja California Sur; lectotype USNM 7156 (79

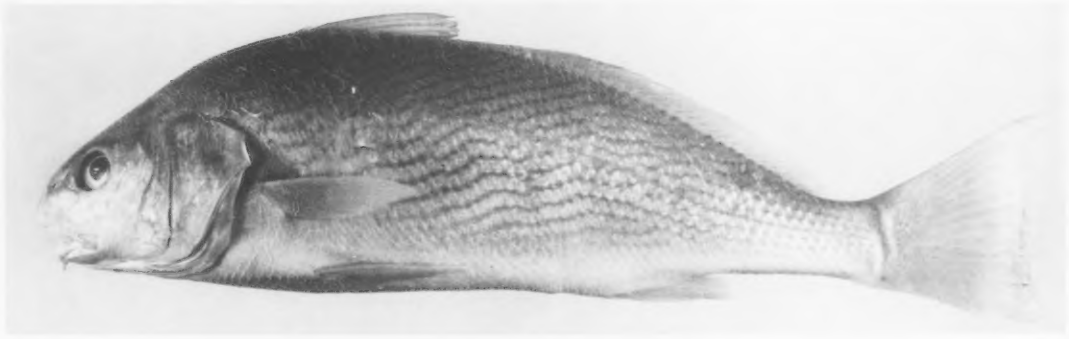

Figure 3
Umbrina roncador, 217 mm SL, SIO 64-65.

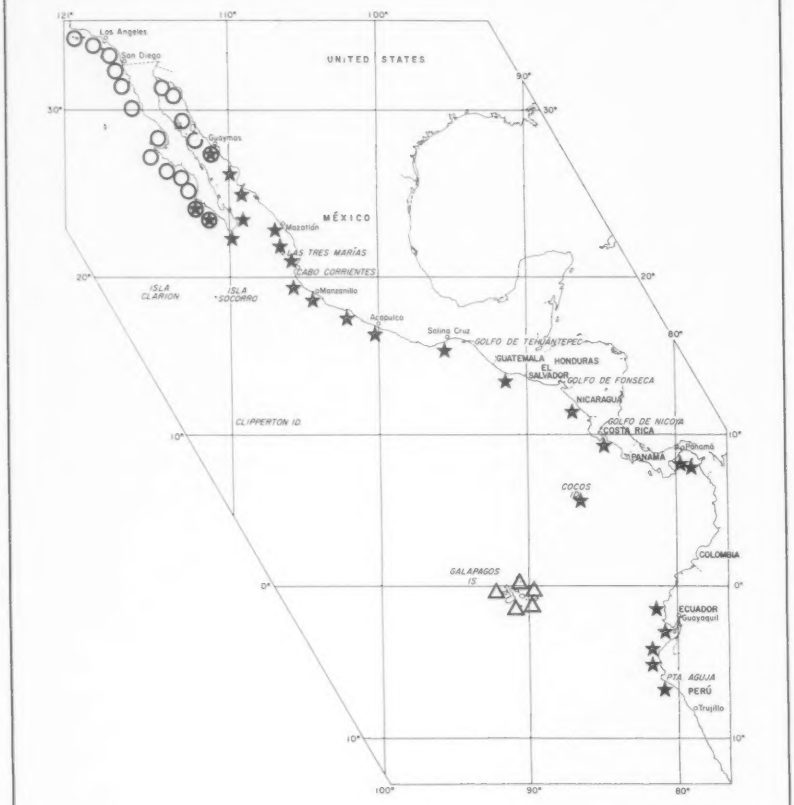

Figure 4
Geographic distribution of *Umbrina roncador* (○), *U. xanti* (★) plus one specimen from Chile at 19°36′S, 70°13′W), and *U. galapagorum* (△).

mm), herein designated; paralectotypes USNM 316653, [removed from USNM 7156] USNM 2996, USNM 3693, USNM 3694, MCZ 35976 [removed from USNM 3693]).

Umbrina sinaloae Scofield 1896:220–221 (original description: syntypes CAS-SU 1632, Mazatlan, Sinaloa, Mexico).

Diagnosis A small species of *Umbrina* (max. length 295 mm) characterized by the following: gill cover dark to black, particularly in area of pseudobranch; peritoneum usually light ventrally, punctate or occasionally dark dorsally; soft dorsal fin rays usually 27–29; soft anal rays usually 6; pectoral rays usually 17–18; procurrent caudal rays usually 8–9 + 8–9; dorsal spines X + I; gill rakers usually 17–19; vertebrae 10 + 15; barbel relatively elongate, slender; length of second anal spine, $\bar{x}$ 12% SL; body depth $\bar{x}$ 29%; eye length, $\bar{x}$ 7%; upper jaw length, $\bar{x}$ 10%; pectoral fin length, $\bar{x}$ 16%.

Figure 5
Umbrina xanti, 188 mm SL, SIO 63-522.

Description Counts and measurements are given in Tables 1–6. Soft rays of second dorsal fin 26–30; soft anal rays 6–7; pectoral rays 14–19; gill rakers 16–21; snout length greater than eye diameter (adults); pigment inside operculum generally appears externally as large, dark spot; dark pigment around pseudobranch evident by 35–40 mm; barbel fully developed by 45 mm, usually knobby between 30 and 45 mm; lateral line scales 48–52, $\bar{x}$ 50.02, SE 0.05; nearly all brown stripes present by 75–80 mm; dark, vertical bars 6–9, occasionally and only on specimens <100 mm; dorsal fin dusky; pectoral, pelvic, anal and caudal fins usually with little or no pigment, caudal occasionally dusky.

Distribution Bahia Magdalena and the southern Gulf of California (south of 27°N) to northern Peru (incl. Isla del Coco, Fig. 4), one specimen from Pisagua, Chile, 19°36′S, 70°13′W. Found in tide pools (juveniles) and along beaches, to 36 m.

Umbrina reedi Günther
Figure 6

Synonymy

Umbrina reedi Günther 1880:25 (original description: holotype BMNH 1919.5.14.283; I. Juan Fernandez, Chile).

Diagnosis A large species of *Umbrina* (max. length 650 mm) characterized by the following: inside gill cover pale to lightly punctate; peritoneum dark ventrally and laterally, lighter dorsally; large, dark spot in axil of pectoral fin; soft dorsal fin rays usually 24–25; soft anal rays usually 9; pectoral rays usually 18; procurrent caudal rays usually 9–10 + 8–9; dorsal spines IX + I; gill rakers usually 19–20; vertebrae 10 + 15; barbel relatively short, stout; length of second anal spine, $\bar{x}$ 14% SL; body depth, $\bar{x}$ 35%; eye length, $\bar{x}$ 7%; upper jaw length, $\bar{x}$ 13%; pectoral fin length, $\bar{x}$ 23%.

Description Counts and measurements are given in Tables 1–6. Soft rays of second dorsal fin 21–26; soft anal rays 8–10; pectoral rays 17–19; gill rakers 18–22; body and caudal peduncle deep; snout length greater than eye diameter at sizes greater than ~150 mm; pectoral fins relatively long; upper jaw long; barbel bulbous at 28 mm, not fully developed until ~120 mm; lateral line scales 49–52, $\bar{x}$ 49.90, SE 0.17; caudal peduncle and midlateral brown stripes evident by 120 mm; dorsolateral stripes undifferentiated on most specimens, appearing as irregular dashes of pigment; dorsal and caudal fins dusky; pectoral, pelvic and anal fins dark (pectorals frequently dusky), lighter on specimens less than ~130 mm.

Distribution Islands off Chile: Islas Juan Fernandez (~33°40′S, 78°55′W) and San Felix (~26°17′S, 80°06′W). From the surf zone to 30 m.

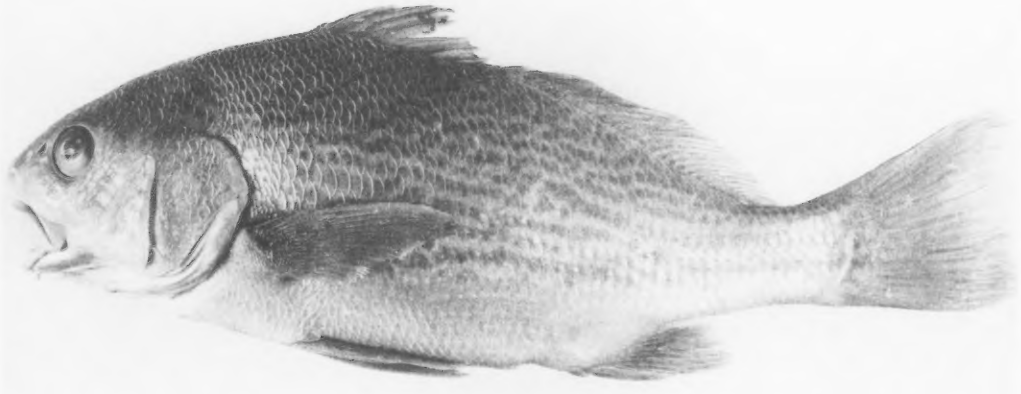

Figure 6
Umbrina reedi, 268 mm SL, SIO 65-657.

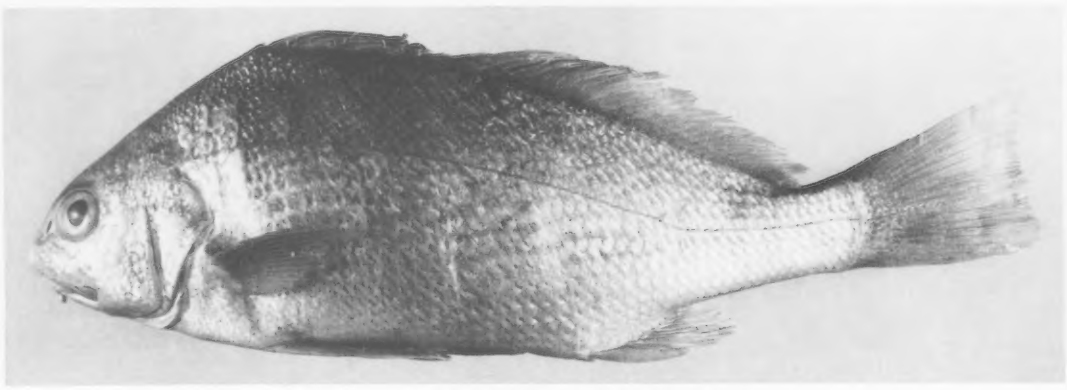

Figure 7
Umbrina dorsalis, 236 mm SL, SIO 62-705.

Figure 8
Umbrina galapagorum, 273 mm SL, SIO 79-51.

Umbrina dorsalis Gill
Figure 7

Synonymy
Umbrina dorsalis Gill 1862:257 (original description: syntypes USNM 3696, Cabo San Lucas, Baja California Sur; lectotype USNM 3696 (77 mm), herein designated; paralectotypes USNM 316654 [removed from USNM 3696]).

Diagnosis An intermediate-sized species of *Umbrina* (max. length 332 mm) characterized by the following: inside gill cover and peritoneum pale to lightly punctate; soft dorsal fin rays usually 30–32; soft anal rays usually 7; pectoral rays usually 16–17; procurrent caudal rays usually 7–8 + 6–7; dorsal spines X + I; gill rakers usually 19–21; vertebrae 10 + 16; barbel relatively long and thick; length of second anal spine, $\bar{x}$ 15% SL; body depth, $\bar{x}$ 38%; eye length, $\bar{x}$ 8%; upper jaw length, $\bar{x}$ 13%; pectoral fin length, $\bar{x}$ 21%.

Description Counts and measurements are given in Tables 1–6. Soft rays of second dorsal fin 28–33; soft anal rays 7–8; pectoral rays 15–17; gill rakers 18–25; eye relatively large, proportionately smaller in larger specimens, generally greater than snout length; upper jaw long; body and caudal peduncle deep; barbel fully developed by 75 mm, bulbous between 30 and 65 mm; lateral line scales 49–54, $\bar{x}$ 51.73, SE 0.15; virtually all brown stripes present by 75 mm, no stripes on speci-

mens <65 mm; 5–8 wide, dark bars (saddles) on specimens 30–65 mm; dorsal and pelvic (posterior) fins dusky to dark; pectoral and caudal fins light to dusky (posterior pectoral fin dark on specimens <45 mm); anal fin dark to dusky.

Distribution South of Bahia Magdalena and in the southern Gulf of California to Equador (Fig. 2). Found in tidepools (juveniles) to ~5 m.

Umbrina galapagorum Steindachner
Figure 8

Synonymy

Umbrina galapagorum Steindachner 1878:20–21 (original description: syntypes MCZ 8601, USNM 120437, James I., Galapagos Is.; lectotype MCZ 8601 (94 mm), herein designated; paralectotype USNM 120437).

Diagnosis An intermediate-sized species of *Umbrina* (max. length 413 mm) characterized by the following: inside gill cover lightly punctate or dusky, usually little or no pigment in area of pseudobranch; brown stripes indistinct or absent; peritoneum pale or lightly punctate; soft dorsal fin rays usually 27–29; soft anal rays usually 6–7; pectoral rays usually 17–19; procurrent caudal rays usually 9–10 + 8–9; dorsal spines X + I; gill rakers usually 18–19; vertebrae 10 + 15; barbel relatively elongate, thin; length of second anal spine, $\bar{x}$ 12% SL; body depth, $\bar{x}$ 29%; eye length, $\bar{x}$ 6%; upper jaw length, $\bar{x}$ 10%; pectoral fin length, $\bar{x}$ 18%.

Description Counts and measurements are given in Tables 1–6. Soft rays of second dorsal fin 26–30; soft anal rays 5–7; pectoral rays 16–20; gill rakers 16–21; snout length greater than eye length; pigment inside operculum occasionally appearing as muted, dark spot; barbel fully developed by 60 mm, bulbous between 30 and ~50 mm; lateral line scales 47–52, $\bar{x}$ 49.73, SE 0.08; faint brown stripes visible at 40–50 mm, occasionally evident to ~100 mm; ~9–10 dark, vertical bars frequently on specimens between ~30 and 95 mm; dorsal and caudal fins usually dusky, caudal occasionally lighter; pectoral, pelvic and anal fins unpigmented to lightly punctate.

Distribution Endemic to the Galapagos Is. (Fig. 4), found near beaches to 18 m.

Umbrina analis Günther
Figure 9

Synonymy

Umbrina analis Günther 1869(1866):426–427 (original description: holotype BMNH 1867.9.23.18, Panama).

Umbrina tumacoensis Wilson 1916:67 (original description: holotype, presumed lost (pers. commun.: M.E. Anderson, CAS, 2 March 1988; B. Chernoff, FMNH, 22 March 1988), paratypes CAS 62852, FMNH 56840).

Diagnosis A small species of *Umbrina* (max. length 231 mm) characterized by the following (based on nine specimens): peritoneum and inside gill cover pale to lightly punctate; soft dorsal fin rays 24–26; soft anal rays 6; pectoral rays usually 17; procurrent caudal rays 8–9 + 7–8; dorsal spines X + I; gill rakers usually 17–18;

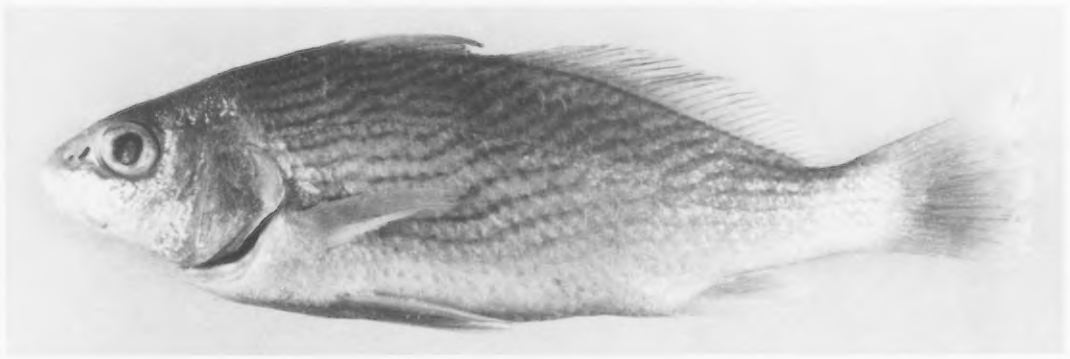

Figure 9
Umbrina analis, 229 mm SL, LACM 33822-32.

vertebrae 10 + 15; barbel relatively short, stout; length of second anal spine, $\bar{x}$ 19% SL; body depth, $\bar{x}$ 32%; eye length, $\bar{x}$ 8%; upper jaw length, $\bar{x}$ 11%; pectoral fin length, $\bar{x}$ 20%.

Description Counts and measurements are given in Tables 1–6. Soft dorsal and anal fin rays as in Diagnosis. Pectoral rays 16–18; gill rakers 16–21; barbel bulbous at 51 mm, more or less fully developed at 82 mm; no brown stripes on a 51 mm specimen, all stripes evident by 82 mm; second anal spine extremely long and thick; caudal peduncle deep; pectoral fins fairly long; lateral line scales 46–50, $\bar{x}$ 47.88, SE 0.44; dorsal and anal fins dusky or dark; caudal fin usually dusky; pectoral and pelvic fins with little or no pigment.

Distribution Known from five collections (one was split), ranging from Costa Rica to Colombia (Fig. 2). No depths recorded.

Umbrina wintersteeni n. sp.
Figure 10

Holotype SIO 60-366, 193 mm; Bahia Almejas, Baja California Sur, F.H. Berry and party, 25 August 1960.

Paratypes 146 specimens (49–298 mm) from 21 collections, all from Mexico: Baja California-west coast: SIO 60-366 (29); SIO 62–126 (10); SIO 64-84 (49); CAS 35536 (4); USNM 316655 (5); AMNH 5514a (1). Gulf of California: UCLA W50-27 (2); UCLA W52-48 (5); UCLA W52-49 (2); UCLA W52-50 (1); UCLA W53-84 (6); UCLA W53-95 (8); UCLA W57-34 (1); UCLA W57-36 (4); UCLA W57-42 (4); SIO 65–281 (3); SIO 76-275 (2); LACM 38104-26 (4); CAS-SU 375 (1); CAS-SU 2855 (3); CAS-SU 47933 (1); AMNH 5498 (1).

Diagnosis A relatively small species of *Umbrina* (max. size 298 mm) characterized by the following: inside gill cover pale to lightly punctate, little or no pigment in area of pseudobranch; peritoneum pale or lightly punctate; soft dorsal fin rays usually 25–27; soft anal rays usually 6; pectoral rays usually 16–18; procurrent caudal rays usually 7–8 + 6–7; dorsal spines X + I; gill rakers usually 17–20; vertebrae 10 + 15; barbel relatively short, stout; length of second anal spine, $\bar{x}$ 14% SL; body depth, $\bar{x}$ 29%; eye length, $\bar{x}$ 7%; upper jaw length, $\bar{x}$ 10%; pectoral fin length, $\bar{x}$ 17%.

Description Counts and measurements are given in Tables 1–6. Soft rays of second dorsal fin 23–28; soft anal rays 5–6; pectoral rays 15–18; gill rakers 14–23; snout length greater than eye length (adults); barbel bulbous at 49 mm, fully developed by ~100 mm; lateral line scales 48–51, $\bar{x}$ 49.14, SE 0.06; faint, brown stripes at 49 mm, nearly all present by 80–90 mm; ~8–11 dark, vertical bars on many juveniles, never on specimens >100 mm; dorsal, pelvic, and anal fins usually dusky to dark (Gulf of California specimens occasionally with light-to-dusky pelvic and anal fins); caudal fin dusky; pectoral fins lightly pigmented; background coloration tan to gold dorsally, grading to white or silver ventrally; dark-brown stripes: 15–20 oblique dorsolaterally, 8–10 more or less horizontal laterally in abdominal area, 4–5 horizontal on lateral caudal peduncle.

Figure 10
Umbrina wintersteeni, holotype, 193 mm SL, SIO 60-366.

Etymology Named for the late John Wintersteen, longtime researcher in the taxonomy of eastern Pacific sciaenids.

Distribution Just north of Bahia Magdalena (25°23′ N, 112°06′W), and the southern Gulf of California from ~27°N to Mazatlan (Fig. 1). Usually collected in bays; thus far, only recorded in depths to ~2m.

Relationships of New World *Umbrina* species

We did not attempt a phylogenetic analysis because we have not seen all *Umbrina* species. In addition, the status and limits of the only recognized sister genus, *Sciaena*, are uncertain. However, morphological similarity allows certain groups of the New World species to be distinguished. *Umbrina bussingi* and *U. milliae* (Atlantic) share several characters: compressed barbel, with anterior, slit-like opening; extremely long pectoral fins; very large eyes; caudal rays longest in middle of fin. They also lack stripes and differ slightly in relative body depth and length of second anal spine; we hypothesize that these are geminate species.

Umbrina analis, *U. broussonnettii* (Atlantic), *U. canosai* (Atlantic), *U. coroides* (Atlantic), *U. dorsalis*, and *U. reedi* share the following characters: relatively deep body; relatively long pectoral fins; dusky to dark anal fin. *Umbrina analis*, *U. canosai*, and *U. reedi* have fairly short, stout barbels and 6, 8, and 9 anal rays, respectively. *Umbrina analis* also has an extremely long, second anal spine. The other three species in this group have relatively slender, elongate barbels and 6 or 7 (*U. dorsalis*) anal rays. *Umbrina dorsalis* also has a relatively large eye and high number of dorsal rays; *U. broussonnettii* and *U. coroides* have low gill raker counts and differ slightly in certain scale and fin counts and pigmentation.

Umbrina galapagorum, *U. roncador*, *U. wintersteeni*, and *U. xanti* share the following characters: relatively elongate body; relatively short pectoral fins; little or no pigment on anal fin (exception: *U. wintersteeni*). Except for *U. wintersteeni*, these species have a somewhat elongate, slender barbel. The inside gill cover of *U. roncador* and *U. xanti* is dark to black and the anal ray counts are 7 and 6, respectively. *Umbrina galapagorum*, which usually lacks stripes (can be faint), and *U. wintersteeni*, which has a short, stout barbel, have 6 anal rays. Although we have no information for some species, juvenile characters (e.g., extreme differences in body depth, pectoral fin pigmentation, dorsolateral pigmentation; Fig. 11) corroborate the latter two major groups (six and four species), with *U. wintersteeni* possibly an intermediate form.

Distribution

As with the species of *Porichthys*, which also are associated with soft bottom (Walker and Rosenblatt 1988), the distributional limits of eastern Pacific species of *Umbrina* generally coincide with zoogeographic boundaries established for rocky shore fishes and other fauna (Springer 1958, Rosenblatt 1967, Briggs 1974, and others). In our area of concern, these boundaries are Point Conception, Bahia Magdalena area, La Paz for the western Gulf of California, and between Guaymas and Mazatlan for the eastern Gulf, Golfo de Tehuantepec area, and northern Peru. *Umbrina roncador* occurs in the northern Gulf of California (north of 27°N) and from Point Conception to the Bahia Magdalena area, which is also the northernmost Baja California (west coast) limit for *U. xanti*, *U. wintersteeni*, and *U. dorsalis*. Both *U. xanti* and *U. dorsalis* are wide-ranging, also occurring from the southern Gulf of California to northern Peru and Equador, respectively. *Umbrina wintersteeni* also is found in the southern Gulf as far south as Mazatlan. *Umbrina bussingi* and *U. analis* are each known from five collections. *Umbrina bussingi* occurs nearly throughout the eastern tropical Pacific (southern Gulf of California to Panama), while *U. analis* apparently is confined to the south (Costa Rica to southern Colombia).

Additional materials examined

Umbrina bussingi 140 specimens (56–257 mm) from 4 collections. **Mexico:** SIO 62-51 (130); SIO 70-160 (1); CAS 36615 (4). **Panama:** LACM 9099-28 (5).

Umbrina roncador 367 specimens (23–338 mm) from 88 collections. **California:** SIO H45-130 (17); SIO H45-162 (3); SIO H46-94 (6); SIO H47-160 (2); SIO H48-101 (1); SIO H51-235 (3); SIO H49-90 (5); SIO 86-63 (2); SIO 88-91 (17); CAS 18797 (8); CAS-SU 12666 (1); CAS-SU 19311 (2); CAS-SU 9913 (4); CAS 19515 (1); CAS 19672 (1); CAS 18532 (1); CAS 18527 (1); CAS 18347 (2); CAS 12934 (2); CAS 18272 (2); UCLA W57-208 (8); UMMZ 162170 (1); UMMZ 177364-5 (1); UMMZ 177457 (1); LACM W58-77 (2); LACM W50-126 (2); USNM 132385 (5); USNM 31316 (1); USNM 31317 (1); USNM 31270 (1); USNM 26872 (4); USNM 26758 (4); USNM 5299 (1); USNM 52978 (1); USNM 59496 (3); USNM 54332 (1); USNM 34781 (1); USNM 132394 (1); USNM 124991 (15); USNM 26849 (1). **Mexico, Baja-west coast:** SIO H46-215A (7); SIO H48-56 (1); SIO H48-55 (1); SIO H52-160 (8); SIO 62-729 (2); SIO H48-48 (12); SIO 62-113 (1); SIO H48-88 (1); SIO H52-137 (8); SIO H52-149 (8); SIO H52-135 (9); SIO 60-364 (5); SIO 60-364 (5); SIO 60-367 (1); SIO H48-91 (1); SIO 62-217 (3); UCLA W61-107 (2); UCLA W52-93 (3); UCLA W51-221 (1); UCLA W52-236 (3); LACM W52-248 (7); LACM W52-270 (3); LACM W51-234 (1); CAS-SU 58622 (8); CAS-SU 47932 (4); CAS W52-245 (8); CAS 11713 (2); CAS W52-183 (1); CAS W52-85 (2); CAS W52-93 (2); CAS W52-101 (2); USNM 54514 (1); USNM 132406 (1); USNM 46730 (2). **Mexico, Gulf of California:** UAZ 57 (1); UAZ 156 (71);

Figure 11
(upper) *Umbrina xanti*, 34 mm SL, SIO 61-232; (lower) *U. dorsalis*, 33 mm SL, SIO 61-232.

SIO 62-217 (3); SIO 63-532 (4); SIO 70-70 (1); CAS-SU 16585 (3); CAS-SU 6327 (1); CAS-SU 187 (1); UCLA W56-76 (3).

Umbrina xanti 397 specimens (20–296 mm) from 63 collections. **Mexico, Baja-west coast:** SIO 62-705 (10); SIO 62-706 (136); SIO 62-707 (2); SIO 62-708 (1). **Mexico, Gulf of California:** UCLA W51-22 (21); UCLA W51-24 (7); UCLA W51-56 (4); UCLA W51-57 (17); UCLA W56-118 (2); UCLA W59-248 (3); LACM W51-41 (1); LACM W51-49 (1); LACM W52-50; LACM W58-46 (1); CAS 2570 (1); CAS 2571 (1); CAS 4489 (1); CAS W51-53 (7); UBC BC 59-216 (1); UBC BC 59-236 (1); USNM 2996 (2); USNM 47443 (4); USNM 47463 (3); USNM 122659 (1); SIO 61-232 (4); SIO 65-349 (1). **Mexico, southern:** MCZ 485 (1); SIO 62-23 (31); SIO 62-28 (2); SIO 62-47 (1); LACM W58-12 (1); UBC BC 57-78 (2); UBC BC 57-85 (1); UBC BC 57-94 (1); UBC BC 57-98 (1);UBC BC 57-108 (1); UBC BC 57-129 (1); UBC BC 60-12 (1); UBC BC 60-13 (1). **Guatemala:** UCR 355-6 (2). **Nicaragua:** UCR 379-13 (1). **Costa Rica, incl. I. Cocos:** UCR 218-39 (1); UCR 259-3 (1); UCR 137-6 (3); LACM 35473-1 (40); SIO 77-89 (38). **Panama:** UCLA W53-283 (3); UCLA W53-285 (3); USNM 82233 (1). **Equador:** USNM 88744 (2). **Peru:** CAS-SU 29850 (2); CAS-SU 37491 (3); UCLA W60-34 (1); UBC BC 56-145 (1); UBC BC 56-149 (1); UBC BC 56-159 (1); UBC BC 56-162 (1); UBC BC 56-165 (1); UBC BC 56-234 (1); USNM 107150 (1); USNM 128009 (8); USNM 128010 (1). **Chile:** Univ. Antofagasta. uncat. (1).

Umbrina reedi 86 specimens (9–650 mm) from 9 collections. SIO 65-623 (1); SIO 65-625 (1); SIO 65-626 (2); SIO 65-655 (2); SIO 65-657 (34); UCLA W66-50 (2); UCLA W66-56 (29); USNM 176411 (7); USNM 88745 (8).

Umbrina dorsalis 93 specimens (28–327 mm) from 25 collections. **Mexico:** SIO 61-232 (12); SIO 61-236 (1); SIO 61-251 (7); SIO 62-23 (3); SIO 62-705 (1); UBC BC 57-100 (1); LACM W55-120 (1); LACM 9044-28 (34); LACM 9045-23 (2); LACM 9051-23 (2); UCLA W51-57 (1); UCLA W53-185 (1); UCLA W59-248 (1). **Costa Rica:** USNM 94000 (1); UCLA W54-168 (2); UCLA W54-172 (1). **Panama:** SIO 90-30 (1); UCLA W53-283 (1); UCLA W53-285 (1); UBC BC 60-117 (1); USNM 144680 (1); USNM 81213 (1); CAS-SU 8113 (2). **Colombia:** UMML Argosy 28, uncat. (1). **Equador:** UMML Argosy 44, uncat. (13).

Umbrina galapagorum 253 specimens (29–395 mm) from 27 collections. MCZ 8597, 8602 (38); MCZ 40448 (1); USNM 153626 (1); CAS 2311 (1); CAS 2313-2318 (6); CAS 2373 (1); CAS 2374-2379 (6); CAS 2384 (1); CAS 2385 (1); CAS 4486 (1); CAS 4657 (1); CAS 4952 (1); CAS 6326 (1); CAS 62979

(2); CAS-SU 24402 (2); CAS-SU 24413 (3); LACM W53-21 (5); LACM W53-28 (9); SIO 62-641 (151); SIO 79-51 (3); UBC BC 56-429 (2); UBC BC 56-437 (1); UCLA W50-219 (2); UCLA W53-144 (1); UCLA W55-314 (1); UCLA W56-325 (1).

Umbrina analis 8 specimens (51–229 mm) from 6 collections. **Colombia:** CAS 62852 (2); CAS 62853 (1); FMNH 56840 (2). **Panama:** USNM 81212 (1). **Costa Rica:** LACM 33822-32 (1); USNM 94612 (1).

Umbrina wintersteeni 9 specimens (56–276 mm) from 7 collections. **Mexico:** SIO 60-365 (3); UCLA W51-18 (1); CAS-SU 4827 (1); CAS W53-94 (1); USNM 29430 (1); USNM 46956 (1); USNM 47463 (1).

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Table 1
Number of soft dorsal fin rays in eastern Pacific species of *Umbrina*. (Asterisks indicate count of primary type.)

	21	22	23	24	25	26	27	28	29	30	31	32	33	$\bar{x}$	SE
U. analis				6	1	2*								24.56	0.29
U. bussingi	5	19*	4											21.96	0.11
U. dorsalis								1	3	15	21	8	2*	30.76	0.14
U. galapagorum						9	59*	89	58	24				28.12	0.07
U. reedi	1	1	4	22*	21	1								24.28	0.12
U. roncador				4	11	72	110	105*	46	6	1			27.32	0.06
U. wintersteeni			1	3	25	37*	23	3						25.95	0.10
U. xanti						13	77	168*	114	30	4	1		28.03	0.04

Table 2
Number of soft anal fin rays in eastern Pacific species of *Umbrina*. (Asterisks indicate count of primary type.)

	5	6	7	8	9	10	$\bar{x}$	SE
U. analis		9*					6.00	—
U. bussingi			30*				7.00	—
U. dorsalis			45*	5			7.10	0.04
U. galapagorum	1	164*	73				6.30	0.03
U. reedi				2	46*	2	9.00	0.04
U. roncador		17	339*				6.95	0.01
U. wintersteeni	2	89*					5.98	0.02
U. xanti		402*	6				6.01	0.01

Table 3
Number of pectoral fin rays in eastern Pacific species of *Umbrina*. (Asterisks indicate count of primary type.)

	14	15	16	17	18	19	20	$\bar{x}$	SE
U. analis			2	14*	2			17.00	0.11
U. bussingi				3	30*	19		18.31	0.08
U. dorsalis		1	65*	33				16.32	0.05
U. galapagorum			1	57	323*	78*	4	18.06	0.03
U. reedi				12	69	19*		18.07	0.06
U. roncador		1	11	175*	422	48	1	17.77	0.02
U. wintersteeni		2	16	147*	17			16.98	0.04
U. xanti	1	1	20	532	192*	8		17.24	0.03

Table 4
Number of total gill rakers in eastern Pacific species of *Umbrina*.

	14	15	16	17	18	19	20	21	22	23	24	25	$\bar{x}$	SE
U. analis			1	5	3			1					17.60	0.43
U. bussingi				1	4	6	11	3	2				19.63	0.23
U. dorsalis					8	35	25	17	7	4	1	1	20.01	0.14
U. galapagorum			1	38	248	126	48	4					18.42	0.04
U. reedi					1	14	11	3	1				19.63	0.16
U. roncador		12	26	48	121	160	120	23	1				18.66	0.06
U. wintersteeni	2	5	12	21	46	43	17	5	4	2			18.32	0.13
U. xanti			10	91	475	90	21	1					18.03	0.03

Table 5

Selected morphometrics of eastern Pacific species of *Umbrina*. HL = head length; SN = snout length; INT = interorbital width; SUB = suborbital width; UJ = upper jaw length; PED = caudal peduncle depth; PEL = caudal peduncle length; PA = preanal length; PF = pectoral fin length; PRD = predorsal fin length; DEP = greatest depth; ASP = second anal spine length.

SL (mm)	Range (10^{-3} SL)												
	HL	EYE	SN	INT	SUB	UJ	PED	PEL	PA	PF	PRD	DEP	ASP
U. analis													
52–231	292–332	67–96	76–103	61–87	50–63	91–120	100–117	220–263	670–721	183–204	362–386	302–342	170–214
U. bussingi													
59–229	338–401	87–108	62–92	70–94	41–57	111–135	76–99	233–265	663–742	239–287	332–417	298–344	154–186
U. dorsalis													
49–327	282–364	57–116	81–103	80–125	37–59	115–173	92–117	235–278	607–652	185–265	344–369	315–378	117–181
U. galapagorum													
30–394	269–354	43–90	86–110	69–96	44–68	87–132	83–103	240–292	610–676	168–190	341–376	249–322	92–172
U. reedi													
85–650	310–360	40–88	83–113	74–101	41–62	110–147	98–122	209–263	634–685	216–247	378–409	306–396	82–159
U. roncador													
22–339	267–342	38–88	71–99	68–102	31–49	93–152	77–116	219–282	641–685	155–195	333–361	247–329	91–146
U. wintersteeni													
30–271	279–344	57–97	83–105	66–100	51–60	92–134	88–112	218–255	648–686	161–199	334–365	261–315	112–168
U. xanti													
20–287	267–316	49–105	69–107	66–99	31–36	85–152	80–113	239–316	605–642	150–172	328–358	235–330	97–157

Table 6

Number of procurrent caudal fin rays in eastern Pacific species of *Umbrina*.

	Dorsal							Ventral						
	6	7	8	9	10	$\bar{x}$	SE	6	7	8	9	10	$\bar{x}$	SE
U. analis			4	2		8.33	0.21		2	4			7.66	0.21
U. bussingi		6	12			7.67	0.11		12	5	1		7.39	0.14
U. dorsalis	1	17	16	4		7.61	0.12	10	22	1			6.73	0.09
U. galapagorum			2	40	12	9.19	0.03		4	33	13		8.18	0.08
U. reedi			1	19	9	9.28	0.05			15	10	2	8.52	0.12
U. roncador			5	29	15	9.20	0.05		1	27	13		8.29	0.08
U. wintersteeni		12	30	2		7.77	0.08	7	27	4			6.92	0.05
U. xanti			16	33	5	8.79	0.08		8	30	12		8.08	0.08

Behavioral reactions of humpback whales *Megaptera novaeangliae* to biopsy procedures

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Abstract.—Accurate and precise descriptions of behavioral indicators of human activities which disturb cetaceans are required to better control adverse human impacts on these animals. We hypothesize that the application of a technique used to remove a small piece of innervated tissue, a biopsy darting procedure, is likely to result in the display of such behavioral indicators. In order to describe such displays, we recorded behavior of 22 humpback whales *Megaptera novaeangliae* before and after biopsy procedures in the southern Gulf of Maine. Reactions varied considerably among animals. Although respiratory responses were not consistent, biopsied whales generally decreased their ratio of surface to dive time and their net movement rate. Hard tail flicks occurred as an immediate reaction in approximately half the cases. Although 31 behaviors were tested for variation, only hard tail flicks significantly increased in either the number of animals that displayed them or the overall frequency of occurrence during postbiopsy reaction periods. While not statistically significant, some increase was noted in the frequency of trumpet blows and tail slashes, while slow swimming and apparent investigative behavior were noted to decrease. The strongest reactions, observed in two cases, occurred when the dart and retrieval line briefly snagged the whale's flukes. These findings complement and extend other studies on the response of baleen whales to human activity at sea.

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The humpback whale *Megaptera novaeangliae* is an endangered species that has been protected from commercial catches since the mid-1960s. Protection from hunting in the North Atlantic portion of its range extends back to 1955. The most recent population estimates suggest close to 10,000 animals remain worldwide, with 5500 in the western North Atlantic (Johnson and Wolman 1985).

The endangered status of this species as well as its affinity for nearshore habits has brought increasing concern that the collective effects of industrial development, resource exploitation, and rapid increase in the whale watching industry could result in displacement, habitat degradation, and behavior modification. It thus has become important to determine whether human activity that is not directly lethal to individual whales could still have deleterious effects on the recovery of this species.

To assess potential deleterious effects of artificial stimuli on the normal behavior of a whale, definitions of disturbed behavior must be clarified. Disturbed behavior can be defined as behavior that results from a noxious stimulus that would not otherwise have occurred. Previous observations have been made under conditions of potential disturbance, such as the presence of boats or divers or the production of underwater noise (Baker and Herman 1982, Malme et al. 1983 and 1985, Bauer and Herman 1985, Richardson et al. 1985). However, a cause-and-effect relationship between the stimulus and a whale's response has been difficult or impossible to achieve, since baseline data on behavioral reactions to clearly noxious stimuli are almost entirely lacking.

Since 1979, humpback whales have been studied intensively in the southern Gulf of Maine to evaluate the demographics, behavior, and ecology of a group of annually-returning individuals (Mayo et al. 1985, Weinrich 1985 and 1986, Clapham and Mayo 1987). In 1983, the University of Florida began studies to determine the genetic characteristics and sex of known individuals in this group of

whales. To obtain the tissue samples for this project, a projectile biopsy dart was used (Lambertsen 1987, Lambertsen and Duffield 1987, Lambertsen et al. 1988).

In an attempt to better understand the disturbance response of large whales, the present study was undertaken to assess the behavioral reaction of humpback whales to the biopsy procedures previously described (Lambertsen 1987). We reason that since the biopsy dart removes a small piece of innervated tissue, it is likely to be perceived by the whale as a noxious stimulus and should cause some observable response. Our results compare the behaviors of the whales before and after exposure to this relatively short-term, moderate-level stressful stimulus.

Materials and methods

Cruises to collect biopsy samples took place each year from 1983 to 1985 on Jeffrey's Ledge or Stellwagen Bank in the Gulf of Maine. In 1983 and 1984 various types of small power vessels (≤12.8 m) were used, including an 11.6 m sportfishing vessel equipped with one Detroit Diesel 671 engine, and a 12.8 m pilot boat with two Detroit Diesel 671 engines. In 1985, a 6.1 m runabout with a 175 hp outboard engine and an 11 m sailing sloop were used simultaneously. The use of two vessels allowed one (the 6.1 m runabout) to be dedicated to collection of behavioral data in the methodology described below. The immediate response of whales to biopsy darting was recorded on two days in 1983, two in 1984, and six in 1985.

The biopsy apparatus used in this study consisted of a tethered retrievable biopsy dart, aimed at the flank below the dorsal fin, fired from a 68 kg crossbow (Lambertsen 1987). A small biopsy punch fitted with internal prongs and attached to the tip of the dart shaft removed the tissue from the animal. A small tissue sample, including both epidermis and dermis, was thus obtained by a cutting action on penetration, and tearing on rebound. Upon penetration of the dart into the whale, a rebound was forced by a 2.5 cm diameter flange set 2 cm back from the tip of the biopsy punch.

In the first 2 years of the study, emphasis was placed on collecting as many biopsies as possible during brief periods at sea. Behavioral observations were collected opportunistically to provide qualitatively classified data on immediate reactions. For comparative purposes, these observations were ranked in a manner similar to that used by Mathews (1986), who studied the reactions of eight gray whales *Eschrichtius robustus* to a similar biopsy procedure. Categories used in this initial analysis included:

No reaction The whale continued its prebiopsy behavior with no detectable change.

Low-level reaction The animal modified its behavior, but displayed none of the overtly forceful behaviors listed as moderate or strong reactions (e.g., immediate dive).

Moderate reaction The animal modified its behavior in a more forceful manner (trumpet blows, hard tail flicks), but gave no prolonged evidence of behavioral disturbance.

Strong reaction The animal modified its behavior to a succession of forceful activities (continuous surges, tail slashes, numerous trumpet blows).

To test statistical differences in reaction levels among age-classes, non- and low-level reaction frequencies were combined, as were moderate and strong reactions. This was necessitated by the low expected values of the frequencies in a chi-square table based on the data in Table 1.

All data from 1983–85 were used to categorize immediate response levels; in 1985, a 30-min prebiopsy **control** period and a 30-min postbiopsy **response** period were defined to standardize a paired data set of respiratory and other surface behaviors. This approach used the vessel dedicated to behavioral data collection to institute a focal sampling technique (Altmann 1974) to allow quantitative comparison of the pre- and postbiopsy focal periods as "paired samples." Upon sighting a group of whales, each individual was distinguished through 7×50 binoculars using distinctive natural markings on the dorsal fin or the ventral surface of the tail flukes (Katona and Whitehead 1981). Because of the necessity of identifying individual respirations and behaviors within the group, dorsal fin shape was used whenever possible during focal samples; permanent identification came from fluke photographs taken during the approach for the biopsy strike. Once individuals were distinguished from one another, a 30-min "control" (i.e., pretreatment) focal sample was then initiated. During this period the engines of the observation vessel were shut down to eliminate engine noise. No approaches closer than 100 m were made prior to the onset of, or during, the 30-min control period. If the whale moved farther than 1000 m from the research vessel, making data collection difficult, the engine was started and approach was made slowly to within ~300 m of the whale. At the conclusion of the 30-min "control" focal sample the whale was then approached at close range (3–40 m) for the biopsy attempt. The same protocol was followed after the biopsy for a comparable "experimental" (i.e., post-treatment) data set, which started at the moment of impact by the dart.

During focal samples, data were collected on four respiratory variables: (1) number of respirations ("blows") during a given surface interval, (2) time between each respiration ("blow interval"), (3) time

the animal spent at the surface ("surface interval"), and (4) time spent below the surface during each dive ("dive time"), defined as the period of submergence following typical sounding behavior (i.e., a prominent, high arching of the back and tail, often followed by bringing the tail flukes above the water surface). The surface interval during which the biopsy strike took place was excluded from our analyses of both the pre- and postbiopsy respiratory variables. We determined (using chi-square goodness-of-fit tests) that the distribution of the observed data was not significantly different from a normal distribution, thus differences between the pre- and postbiopsy values were compared using two-tailed paired t-tests (Zar 1984). Surface-interval to dive-time ratios were calculated for each whale during pre-biopsy and postbiopsy focal samples, and compared using a Wilcoxon sign rank test (Zar 1984). The surface-interval/dive-time ratio integrates several respiratory values into a single measure of the respiratory "strategy" for each individual.

LORAN-C positions, which have an error of ~30 m in the study area (Day 1983), were used in estimating the net rate of movement of a whale as defined by its surfacings. LORAN positions were recorded at the start and end of each focal sample. With each LORAN-C reading, the bearing to the whale to the nearest 5 degrees and the visually-estimated distance from the vessel to the whale were also recorded. This information was used to correct the LORAN-C data if the whale was >30 m from the vessel, which was likely given the limitations of vessel movement during focal samples described above. To estimate the net movement rate, the distance between the first and last calculated whale positions within each focal sample period was divided by the elapsed time (30 minutes), yielding a net movement rate in knots. Actual swimming speed could not be determined due to uncertainty about the direction of a whale's movement underwater or the linearity of its track. Results between pre- and postbiopsy periods were compared using a Wilcoxon sign rank test (Zar 1984).

Photographs of the dorsal fin and tail flukes of individual whales were taken upon approach for biopsy. Each whale was identified using the catalog of Gulf of Maine humpback whales kept at the Cetacean Research Unit, where individuals are assigned a two-letter, one-number file code. If the animal could not be identified in the catalog, it was assigned a three-digit code. When possible, each animal was assigned to one of the following age groups: juvenile (1–3 yr), adolescent (4–6 yr), or adult (>6 yr). Age classifications were based on previous and/or subsequent repeated annual observations of the same individuals by the authors from calf year (used for juveniles and adolescents), sightings of the individual as an initially small and subsequently larger animal (juveniles and adolescents), or annually repeated sightings of an individual with no appreciable growth over several years (adults). If an animal was sighted only during the year in which it was biopsied, it was not classified by age-class.

During focal samples collected in 1985, a total of 30 behavior types were observed and analyzed. Behavior types were defined using an ethogram for humpback whales developed by the Cetacean Research Unit prior to this study (unpubl. data). The probability that any given behavior was displayed by more or fewer animals in the pre- vs. postbiopsy focal samples was tested using the binomial distribution (with the probability of each period containing an occurrence of the behavior assumed as 0.5), while the change in frequency of each behavior in individuals, given that the behavior was observed at all, was compared using Wilcoxon signed rank tests (Zar 1984). All 30 behaviors were tested for variation. Many of the behaviors did not show any variation between control and response periods, and therefore are not described in detail. These were belly-up rolls, breaches, bubble clouds (bubble clouds followed by obvious surface feeding), bubble cloud behaviors (bubble clouds not followed by obvious surface feeding), defecations, flipper flares, flipper flicks, flipper in air, flukes, half flukes, hangs, high flukes, high head-ups ("spyhops"), lobtails, logging, low flukes, quarter rolls, single bubbles, snakes (a twisting of the body), surges, tail breaches, and passing under a boat. Definitions of those behaviors which either varied significantly in frequency or showed some notable variation in the frequency of display following the biopsy procedure are the following:

Back rise Animal breaks surface while swimming, with no accompanying exhalation.

Belly-up lobtail Animal, ventral side up, elevates tail into the air, then slaps the water surface with the dorsal surface of its flukes.

Hard tail flick Animal rapidly and forcefully flexes tail up and down one time during otherwise normal swimming behavior; much spray can be thrown; flukes clear surface. The hard tail flick is faster and presents a less regular arching movement of the tail than a lob-tail.

Low head-up Animal lifts head into air at 30–45° angle to surface.

Sounding dive Animal arches its back in a typical diving posture but does not bring its tail flukes above the surface.

Tail rise Animal slowly straightens its caudal peduncle at the surface during normal swimming.

Tail slash Animal moves tail forcefully from side to side, flukes at or just below the surface; creates white water frothing.

Trumpet blow Loud, broad-band, wheeze-like sound made during exhalation at the surface.

In addition, the following behaviors showed a variation in frequency during the special case of SI4's reaction (discussed below):

Belly-up Animal rolls so that the whale has its ventral surface exposed above the surface (often for longer than a second).

Half fluke Animal rolls on its side exposing one fluke above and perpendicular to the surface.

Results

Immediate behavioral reactions, or the absence thereof, to the biopsy procedure were recorded for 71 biopsy strikes during the period 1983–85. Of these, 22 (recorded in 1985) are paired samples including a 30-min prebiopsy and 30-min postbiopsy focal sample. Two cases contained clearly unusual reactions, including one from the 1985 paired samples. These cases are discussed separately. This leaves 21 paired samples of behavioral data; however, in five cases some respirations could not be accurately assigned to a whale within the focal group, leaving 16 paired samples of complete respiratory data for analysis.

Immediate behavioral response

Of the 71 total biopsy attempts for which immediate behavioral reactions were recorded, 7.0% involved no behavioral reaction, 26.8% involved a low-level reaction, 60.6% involved a moderate reaction, and 5.6% involved a strong reaction (Table 1). All the strong reactions involved snagging of the flukes by the monofilament line attached to the biopsy dart.

Immediate dives were the most common response to the biopsy dart striking the animal, observed in 35 (49.2%) cases, hard tail flicks were present in 34 (47.8%), and trumpet blows were observed in 31 (43.6%) cases. Less than 20% of all reactions involved immediate surges or visually detectable increases in swimming speed.

Although an immediate dive was a frequently observed response, this may have been due to the time it took to approach the whale for the biopsy strike, i.e., the whale would have taken a dive at that point regardless of the biopsy attempt. However, the mean number of blows (4.89) during the surfacing interval in which the biopsy dart was fired was significantly lower than in the accompanying complete surfacings immediately prior to the biopsy attempt (7.17) (paired t-test: t −2.76, 15 df, p 0.015),suggesting those dives which occurred immediately after the strike of the biopsy dart were initiated as a response to the biopsy procedure.

Table 1
Qualitative ranking of intensity of behavioral responses in humpback whales *Megaptera novaeangliae* to biopsy procedures. NR = No reaction.

	NR	Low	Moderate	Strong	Total
Juveniles (1–3 yr)	2	3	10	3	18
Adolescents (4–6 yr)	0	4	6	0	10
Adults (>6 yr)	3	12	23	1	39
Unclassified	0	0	4	0	4
Total	5	19	43	4	71

Study animals could be categorized by age-class in 68 of the 71 trials. There was no significant difference in the intensity of reactions by age-class (χ^2 2.88, 3 df, p 0.41) (Table 1). However, 3 of the 4 reactions we ranked as strong were from juveniles. Also, strong reactions were always associated with a snagging of the retrieval line on the animals' flukes.

Respiratory and dive variables

There were no significant differences between pre- vs. postbiopsy focal samples for any of the four respiratory variables (paired t-tests (15 df): blow interval t 0.82, p 0.42; number of blows/surfacing interval t −0.93, p 0.36; surfacing interval t 1.65, p 0.11; dive time t 0.61, p 0.55). There was a significant decrease in the surface-interval/dive-time ratios during postbiopsy focal samples (Wilcoxon signed rank test, Z −2.11, p 0.03).

Substantial individual variation was found in respiratory variables. Seven animals (43.8%) showed a decrease in their mean blow interval following the biopsy procedure, and eight (50.0%) showed an increase (Table 2). Eleven individuals (68.8%) showed a decrease in the number of blows per surfacing, while in only four (25.0%) did it increase (Table 3). Similarly, eleven whales (69.0%) reduced their surface interval in the postbiopsy period, while in five (32.0%) this variable increased (Table 4). Finally, eight of the 16 individuals (50.0%) were found to decrease their dive times during the postbiopsy period, while in the other eight (50.0%) it increased (Table 5). The surface-interval/dive-time ratio also showed a decrease in 9 of the 16 animals (57.0%), while in 5 (32.0%) there was no change and in 2 (13.0%) there was an increase (Table 6). Based on binomial distribution, any case with 9 or more, or 2 or less, animals showing a change in a particular

direction would be significant at p 0.07 (based on 11 samples, ignoring the 5 that showed no change), indicating a significant decrease in the surface-interval/dive-time ratio in the sample.

To determine whether the immediate behavioral response to the biopsy dart affected subsequent

Table 2
Mean blow intervals (s) and standard deviations in humpback whales *Megaptera novaeangliae* during focal samples before and after biopsy procedures. Each individual whale is represented by a two-letter one-number code or a three-number code.

	Prebiopsy			Postbiopsy			
Animal	N	$\bar{x}$	SD	N	$\bar{x}$	SD	Difference
CO7	18	27.9	35.9	17	22.0	14.8	−5.9
SE6	11	49.2	43.2	15	46.3	45.9	−2.9
ZE1	19	36.4	23.7	23	26.8	23.4	−9.6
547	23	34.7	27.2	18	38.2	18.5	3.5
SW1	26	23.3	24.0	21	32.8	16.5	9.5
TH6	22	28.3	15.8	16	28.9	22.5	0.6
LA5	17	22.3	12.1	25	22.3	15.5	0.0
TR2	23	19.3	20.5	26	24.5	14.4	5.2
KE2	12	83.7	74.3	11	51.7	37.1	−32.0
ME1	22	14.5	2.6	19	16.0	2.0	1.5
CO9	22	16.3	5.3	21	15.9	4.0	−0.4
ST1	19	34.6	23.8	30	33.3	26.4	−1.3
OC1	38	30.4	20.4	36	32.6	27.1	2.2
SM1	32	27.8	22.8	21	33.7	27.1	5.9
CI1	23	14.3	5.1	17	18.3	13.3	4.0
RA6	12	31.8	20.3	10	19.3	7.1	−12.5
Sample		30.9	16.8		28.9	9.5	−2.0

Table 3
Mean number of blows per surface interval in humpback whales *Megaptera novaeangliae* during focal samples before and after the biopsy procedure. Each individual whale is represented by a two-letter one-number code or a three-number code.

	Prebiopsy			Postbiopsy			
Animal	N	$\bar{x}$	SD	N	$\bar{x}$	SD	Difference
CO7	4	4.4	1.1	4	8.6	4.2	4.2
SE6	2	8.3	6.0	5	3.7	1.9	−4.6
ZE1	3	10.0	6.0	5	5.0	3.7	−5.0
547	5	4.7	2.9	5	4.0	2.0	−0.7
SW1	3	5.8	1.0	4	5.8	1.7	0.0
TH6	5	6.5	2.4	6	6.0	2.9	−0.5
LA5	8	4.2	2.8	5	2.8	2.2	−1.4
TR2	3	8.7	3.1	4	7.3	3.0	−1.4
KE2	4	4.0	2.5	5	3.2	2.3	−0.8
ME1	7	4.1	1.9	2	8.0	2.8	3.9
CO9	5	5.4	2.5	11	2.9	1.6	−2.5
ST1	7	3.9	1.5	5	7.0	6.6	3.1
OC1	4	10.5	6.4	5	8.2	6.8	−2.3
SM1	6	6.3	4.3	5	5.2	4.8	−1.1
CI1	6	4.4	1.8	2	2.3	1.5	−2.1
RA6	4	2.3	1.7	4	3.5	1.3	1.2
Sample		5.8	2.4		5.2	2.1	−0.6

Table 4
Mean surface interval length (s) in humpback whales *Megaptera novaeangliae* during focal samples before and after the biopsy procedure. Each individual whale is represented by a two-letter one-number code or a three-number code.

	Prebiopsy			Postbiopsy			
Animal	N	$\bar{x}$	SD	N	$\bar{x}$	SD	Difference
CO7	4	117.7	135.2	4	196.4	123.2	78.7
SE6	2	399.0	291.9	5	140.8	156.1	−258.2
ZE1	3	369.3	251.4	5	110.3	119.0	−259.0
547	5	158.0	115.7	5	121.0	58.5	−37.0
SW1	3	115.5	49.3	4	199.5	87.0	84.0
TH6	5	206.6	96.2	6	135.8	94.8	−70.8
LA5	8	62.5	71.5	5	46.3	21.6	−16.2
TR2	3	154.0	104.5	4	168.0	106.6	14.0
KE2	4	256.8	177.2	5	135.4	106.5	−121.4
ME1	7	61.1	47.2	2	122.0	42.4	60.9
CO9	5	76.0	41.4	11	29.6	19.6	−46.4
ST1	7	113.9	104.6	5	222.4	244.1	108.5
OC1	4	390.3	292.3	5	264.4	282.4	−125.9
SM1	6	216.8	157.3	5	138.6	163.8	−78.2
CI1	6	57.5	35.8	2	36.1	49.9	−21.4
RA6	4	64.5	21.5	4	32.0	14.4	−32.5
Sample		176.2	120.1		131.1	70.0	−45.1

Table 5
Mean dive interval length (s) in humpback whales *Megaptera novaeangliae* during focal samples before and after the biopsy procedure. Each individual whale is represented by a two-letter one-number code or a three-number code.

	Prebiopsy			Postbiopsy			
Animal	N	$\bar{x}$	SD	N	$\bar{x}$	SD	Difference
CO7	4	92.2	84.6	4	194.8	112.7	102.6
SE6	2	171.3	94.7	5	177.2	79.8	5.9
ZE1	3	181.0	23.5	5	145.4	87.0	−35.6
547	5	146.7	113.6	5	314.0	76.7	167.3
SW1	3	394.7	149.8	4	145.8	121.8	−248.9
TH6	5	127.5	22.9	6	200.0	88.3	72.5
LA5	8	254.5	35.4	5	216.5	48.9	−38.0
TR2	3	412.5	9.2	4	391.3	253.4	−21.2
KE2	4	228.5	90.6	5	125.0	90.6	−103.5
ME1	7	250.5	125.5	2	565.5	38.9	315.0
CO9	5	161.0	129.9	11	120.3	62.9	−40.7
ST1	7	122.0	107.1	5	204.6	251.3	82.6
OC1	4	153.8	75.7	5	124.3	127.8	−29.5
SM1	6	96.7	57.7	5	199.0	109.2	102.3
CI1	6	170.3	35.0	2	113.6	76.9	−56.7
RA6	4	324.8	115.4	4	355.0	167.5	30.3
Sample		205.5	98.9		224.5	18.4	19.0

responses in respiratory variables, we examined separately those animals that reacted to the biopsy strike with an immediate hard tail flick (n 9), the most obviously forceful immediate response to the biopsy strike. This subset would therefore eliminate those animals who may have not been affected by the biopsy strike. However, variation among individuals during the postbiopsy period was not appreciably different from that portion of the sample where no hard tail flick was observed (binomial test). Hence, the occurrence of an immediate forceful response to the biopsy procedure does not appear to be associated with subsequent changes in respiratory variables.

Net movement rate

For 11 of the 21 animals, LORAN-C fixes allowed a calculation of the animal's net movement rate in pre- and postbiopsy focal samples. During the prebiopsy sample, only two animals showed values >1kn. During the postbiopsy period, the average rate did not increase significantly (Wilcoxon signed rank test, Z −1.82, p 0.07). However, only three animals had rates <1kn, and a generally increasing trend was recorded (Table 7).

Other behavioral responses

To consider changes in behavior elicited by the biopsy procedure, the possibilities of introducing new behaviors or altering display rates of regularly observed behaviors were both considered. The former was examined using the number of pre- and postbiopsy focal samples during which each behavior type was observed, while the latter was examined using the direction and magnitude of changes in observed behavior types within individual paired samples (Tables 8, 9). Only one of the 30 tested behavior types showed significant differences between the pre- and postbiopsy period.

Eleven of the 21 (52.3%) postbiopsy focal samples contained a hard tail flick, while the behavior was not observed in the prebiopsy focal samples (binomial distribution, $p<0.001$). Only once was a hard tail flick observed more than one time after a biopsy strike. This also was the only case in which the hard tail flick was not an immediate response to the biopsy dart. The percentage of biopsy strikes where the reaction included a hard tail flick among paired samples was not significantly different from that of the larger 1983–84 sample, where 34 of 50 animals displayed the hard tail flick (χ^2 1.54, 1 df, p 0.21).

As was the case in the number of 30-min samples in which a behavior was displayed, only hard tail flicks showed a significant increase in frequency during the postbiopsy period (binomial distribution, p 0.001). While results were not significant, one or more animals also showed notable increases in the numbers of trumpet blows, tail slashes, and belly-up lobtails following the biopsy procedure; similar nonsignificant but notable decreases were seen in back rises, tail rises, and low head-ups (Tables 8, 9). The latter three behaviors are associated with slow, unhurried travel, resting, or interest in nonessential environmental stimuli (e.g., boats, seaweed).

Table 6

Mean surface-interval/dive-time ratio in humpback whales *Megaptera novaeangliae* during focal samples before and after the biopsy procedure. Each individual whale is represented by a two-letter one-number code or a three-number code.

Animal	Prebiopsy	Postbiopsy	Difference
CO7	1.3	1.0	−0.3
SE6	2.3	0.8	−1.5
ZE1	2.0	0.8	−1.2
547	1.1	0.4	−0.7
SW1	0.3	1.4	1.1
TH6	1.6	0.7	−0.9
LA5	0.2	0.2	0.0
TR2	0.4	0.4	0.0
KE2	1.1	1.1	0.0
ME1	0.2	0.2	0.0
CO9	0.5	0.2	−0.3
ST1	0.9	1.1	0.2
OC1	2.5	2.1	−0.4
SM1	2.2	0.7	−1.5
CI1	0.3	0.3	0.0
RA6	0.2	0.1	−0.1
Sample	1.1	0.7	−0.4

Table 7

Net movement rate (kn) in humpback whales *Megaptera novaeangliae* during focal samples before and after the biopsy procedure. Each individual whale is represented by a two-letter one-number code or a three-number code.

Animal	Prebiopsy	Postbiopsy	Difference
CO7	0.5	1.7	1.2
SW1	0.7	1.5	0.8
TR2	0.8	2.0	1.2
ME1	0.8	4.5	3.7
ST1	0.5	0.6	0.1
OC1	0.9	0.6	−0.3
SM1	0.8	1.3	0.5
RA6	3.8	1.5	−2.3
BI1	1.5	3.8	2.3
PE4	0.5	1.1	0.6
SI4	0.5	0.7	−0.2
Sample	1.0 (SD 0.9)	1.7 (SD 1.3)	0.7

Table 8

Frequency of various behavior types in humpback whales *Megaptera novaeangliae* before the biopsy procedure ("control period"). Each individual whale is represented by a two-letter one-number code or a three-number code.

	CO7	SE6	ZE1	547	SW1	TH6	LA5	TR2	KE2	ME1	CO9	ST1	OC1	SM1	CI1	RA6	BI1	CR1	SI4	FL2	PE4	Total
Half fluke				2								1		1				1				5
Quarter roll						1																1
Bubble cloud																					2	2
Single bubble																						0
Breach									1					1								2
Back rise	9	3	11	2	1	1	2					1	7	3			1	1				42
Tail breach									2													2
Belly up												1										1
Belly-up lobtail																						0
Cloud behavior												2									8	10
Defecation																					1	1
Flipper flick																						0
Flipper in air												2										2
Flipper flare																						0
Fluke	3			2	2	2	1	3	2		4	4	3	2	1	4	3		3	4	5	7	55
Hang																						0
High fluke												1										1
High head-up	1											1										2
Hard tail flick																						0
Low fluke				1		1								1			1		1	3	1	9
Low head-up		3	4			1						1										9
Log (min)		9.3	9.5																			19
Lobtail														1				1	1			3
Snake																			1			1
Sounding dive	4	2		2	2			1	2	1	3	1	3	3	2		1	1			1	29
Surge					2											1	1					4
Tail rise		2		3		3	1		3	1		2	1	2	1		11	1	7		2	44
Trumpet blow				4	1	2				2	2	3	2	1		2	4	5	3	4		38
Tail slash				1		1				1										7		3
Under boat												1						1				2

Feeding behavior was observed with equal frequency in both the pre- and postbiopsy samples. Those animals engaged in feeding activity showed virtually no reaction to the biopsy attempt. A hard tail flick was never observed from an animal engaged in feeding activity, although it was observed during all other prebiopsy behavioral modes. Logging (resting) behavior was also displayed equally in both sample periods; however, whales logging when biopsied were observed to temporarily interrupt their logging period immediately following the biopsy.

Special cases

Two special cases of behavior modification were noted in conjunction with the biopsy procedure. Both involved the monofilament retrieval line becoming briefly snagged around one of the flukes of the whale. These represent the most vigorous and prolonged reactions to the biopsy procedure we observed.

In one case, for a period of time after the biopsy strike (~16 min) the line remained looped around the tip of one fluke of the tail and the animal behaved abnormally, swimming at elevated speeds (6–7 knots) in a roughly S-figured course. Although visually estimated, this speed appears higher when compared with values reported above. Another whale accompanied this animal in its vigorous swimming.

SI4 exhibited another unusual reaction after a biopsy (at a different time than the reaction reported for the same individual in Table 9). This whale had been associated with CR1 during the day of the biopsy effort; 40 min prior to the first strike of SI4, CR1 was sampled with little reaction. When SI4 was first struck by the biopsy dart its reaction was also minimal, but a tissue sample was not obtained. The next shot (29 min later) missed the whale, but involved a momentary snag of the line on the animal's tail stock. In response, the animal started to trumpet blow with increasing frequency but remained stationary and was easily approached. A third firing of the biopsy dart 11 min later was successful in obtaining a tissue sample.

Table 9

Frequency of various behavior types in humpback whales *Megaptera novaeangliae* following the biopsy procedure ("reaction period"). Each individual whale is represented by a two-letter one-number code or a three-number code.

	CO7	SE6	ZE1	547	SW1	TH6	LA5	TR2	KE2	ME1	CO9	ST1	OC1	SM1	CI1	RA6	BI1	CR1	SI4	FL2	PE4	Total
Half fluke				3	1	2							1	1							1	9
Quarter roll			1			1															1	3
Bubble cloud																					2	2
Single bubble			2																			2
Breach																						0
Back rise	1	1	1	1	3	1	1		3			1	3	4								20
Tail breach									2													2
Belly up				1																		1
Belly-up lobtail									20													20
Cloud behavior																					7	7
Defecation																						0
Flipper flick														1								1
Flipper in air																						0
Flipper flare												1										1
Fluke	4	2	2	1	2	4	1	2	3	2	7	2	2	2	3	2		1	2	4	7	55
Hang												1										1
High fluke				1						1		1			1	1						5
High head-up																						0
Hard tail flick				1	1	1	1	1	1				1	2	1		1	1				12
Low fluke			1				1				1	1	1	1	2		1	2		1	2	14
Low head-up			1											1								2
Log (min)													3	3				13				19
Lobtail									4		1				1						1	7
Snake																						0
Sounding dive		4	6		2		3	1	5		2	2	1	4	5		1			3	5	44
Surge					1								1	1								3
Tail rise	3		2	2	3	2		1	1		1	1	1	4	3		2	2	2	1		31
Trumpet blow	1	1		3	2	8	1	1	1		1	1	4	9	5			4		5	10	57
Tail slash		1				2		1						1					1			11
Under boat																			1		1	2

Following the final biopsy attempt, SI4 started a series of stereotypic actions. Every 45–60 s, the animal would trumpet blow loudly, then tail slash or low-lobtail (a quick, low version of lob-tailing behavior), surge forward, and roll sideways with great force, often rolling ventral-side-up and spiraling underwater. Periods of submergence were <30 s in all cases. The swimming path was erratic, but the animal was never >100 m from the vessel. It passed immediately below the vessel twice, repeatedly surfacing on alternating sides of the boat. Swimming speed appeared greater than normal, although net movement in any one direction was minimal. During the same period CR1 appeared placid, although it did trumpet blow three times. After 14 min, the vigorous behavior of SI4 suddenly ended, and both animals started logging side by side. At this point, they were within 25 m of the vessel. Logging behavior continued for at least 15 min at which point the observation was terminated.

In order to compare the intensity of SI4's reaction with the sample analyzed above, we compared the rate at which it displayed various behavior types in the postbiopsy focal sample with the larger paired sample (n 21). To obtain a mean number of occurrences of each behavior type in the postbiopsy period, the total number of observations of each behavior type was divided by the number of paired samples (Table 10). From these data, it is clear that unusually high numbers of tail rises, trumpet blows, half flukes, belly-ups, lobtails, tail flicks, and tail slashes occurred in SI4's response.

Discussion

The results of this study indicate that behavioral reactions of individual whales to the biopsy procedure are detectable but do not appear to be severe. Immediate reactions (hard tail flicks) took place in >50% of 71 biopsy strikes, which is especially noteworthy given the rarity of this behavior in any other context. However, no significant difference was seen in most of the 30 observed behaviors in 30-min pre- and postbiopsy

Table 10

Frequency of various behavior types observed in a humpback whale *Megaptera novaeangliae* (animal SI4) subjected to repeated strikes of the biopsy dart compared with mean for the entire study population (not including SI4). Values given represent average over the 30-min postbiopsy focal sample. *N* of study population = 21.

Behavior	Study population	SI4
Half fluke	0.42	19
Quarter roll	0.14	2
Bubble cloud	0.09	0
Single bubble	0.09	1
Breach	0.00	0
Back rise	0.95	7
Tail breach	0.08	1
Belly up	0.04	12
Belly-up lobtail	0.95	0
Cloud behavior	0.33	0
Defecation	0.00	0
Flipper flick	0.04	1
Flipper in air	0.00	3
Flipper flare	0.04	2
Fluke	2.61	5
Hang	0.04	0
High fluke	0.23	0
High head-up	0.00	1
Low fluke	0.65	0
Low head-up	0.09	4
Log (min)	0.90	0
Lobtail	0.33	26
Snake	0.00	0
Sound	2.09	0
Surge	0.14	6
Tail flick	0.57	11
Tail rise	1.47	13
Trumpet blow	2.71	29
Tail slash	0.52	11
Under boat	0.09	2

behavioral focal samples. A significant decrease in the ratio of surface interval to dive time followed the biopsy procedure. Although not statistically significant, increases in trumpet blows and, to a lesser extent tail slashes and sounding dives, were noted following biopsy strikes, as were decreases in the amount of slow swimming and some nonessential behaviors.

Two of the behavior types that were noted to increase, trumpet blows and tail slashes, have been previously suggested to be agonistic (Baker and Herman 1984, Watkins and Wartzok 1985). A tail slash may be used by a humpback whale as a means of aggression against another whale in what has been interpreted as courtship battles (Baker and Herman 1984). Norris and Reeves (1977) identify "tail swishing" (our "tail slashing") as one of the more common behavioral responses to harassment.

The behaviors elicited by the biopsy procedure in most cases are not intrinsically different from those behaviors which occur naturally in this species. Thus we emphasize that it may be the change in frequency of behaviors that should be viewed as indicative of "affected" behavior, rather than the occurrence of such displays *per se*. The one notable exception is the hard tail flick, which rarely has been observed other than in response to the biopsy procedure.

The possibility exists that the hard tail flick reaction we observed is a reflex response. This reaction typically occurred at the instant of dart impact and thereafter was rarely repeated. Moreover, in some individuals a single hard tail flick at the time of the biopsy was followed by a period during which no other behavioral change was observed. A reflex response is consistent with our finding of no correlation of respiratory variation with the occurrence of this reaction.

While some of the hard tail flicks may have been purely reflexive, the same behavior was seen once in response to an extremely close vessel approach when no physical contact was made. Further, a similar reaction was reported by Watkins (1981), who labeled it a "startle response." Hence it is uncertain whether this behavior is reflexive or cognitive. It may have both components.

In other studies of whale disturbance in response to noxious stimuli, both Watkins (1981) and Mathews (1986) mention the approach of the vessel as contributing to the reaction of the animal. We made every effort to diminish vessel effects. Both previous studies were conducted from power-driven vessels approaching at moderate to rapid speeds. In over half of our paired samples, data were collected from the relatively silent approach of a sailboat. Those approaches made under power in paired samples were done at slow speed. Further, we limited movement of the research vessels near whales, except in the brief approach for the biopsy, to lessen effects of vessels. While the effect of the vessels was minimized, this approach is a necessary part of the biopsy procedure and need not be considered separately in an analysis of responses.

Our results are comparable with those found by Mathews (1986), who examined the response of eight gray whales to a similar biopsy procedure. Both studies established great variability in the reaction of whales to biopsy procedures. One clear difference is that the blow interval of gray whales showed a significant increase in the postbiopsy period, while that of the humpback whales we studied did not. Even so, four of the eight gray whales studied by Mathews (1986) showed a reduction in their surface-interval/dive-time ratios, as did 57.0% of the larger sample; only one gray whale showed an increased surface-interval/dive-time ratio.

There have been other studies of the response of humpback whales to human-induced stimuli. In Alaska, 17 humpback whales exhibiting "affected" behavior associated with the proximity of vessels increased their mean and maximum dive intervals, while their mean blow interval decreased (Baker and Herman 1982). In comparison, although the whales in our study did not consistently increase the length of their dives following the biopsy, blow intervals decreased slightly. In both studies, whales decreased surface-interval/dive-time ratios on average. The whales in our study and in that of Baker and Herman (1982) also responded with an increased rate of net movement.

Our results generally agree with other studies of the reactions of baleen whales to a variety of human-induced stimuli. Richardson et al. (1985) found that bowhead whales *Balaena mysticetus* respond to a variety of man-made stimuli (drillships, vessels, aircraft) by reducing their surface-interval/dive-time ratios. Swimming speeds increased in response to vessel traffic. Migrating gray whales, by comparison, have been reported to slow down as their migration route took them toward simulated offshore industrial activity (Malme et al. 1983, 1985). Bauer and Herman (1985) found that humpback whales on Hawaiian breeding grounds reduced their surface interval as vessels approached closely. The blow interval decreased as either the proximity or the number of vessels increased. Similarly, pod speed increased as vessels approached. Hence, the net effect in all these studies was the same as we have found; namely, that the animal avoids the source of the stimulus.

It is important to note that the reactions we describe in most cases were elicited by a noxious stimulus of brief duration and low-to-moderate amplitude. On this basis, our findings likely underestimate the effects of a more prolonged noxious stimulus, or one of greater force. For example, extreme responses, including escape, hard tail flicks, and immediate submergence, has been documented in harpooned right whales *Eubalaena glacialis* (Scammon 1874) and fin whales *Balaenoptera physalus* (Lambertsen and Moore 1983).

In the context of current management problems, the response of a whale to a prolonged sublethal noxious stimulus is a critical issue, as habitat intrusion may establish conditions of continuing, if not constant, exposure to diverse noxious stimuli. Recognizing this, Bauer and Herman (1985) considered the relationship of stimulus amplitude and duration (expressed as the number of whale-watching vessels and the length of time a whale group was in close proximity to whale-watching vessels) to elicited responses in their study of the effects of vessel traffic on humpback whales. In both cases, their data indicate a graded response in strenuous episodes of breaching, lobtailing, and flippering behavior and in movement away from the path of vessels.

Although our present study was not designed to evaluate the effects of increasing stimulus duration, including that approximated by stimulus repetition, the special case of SI4 is illuminating. Its progressively increasing reaction to repeated biopsy strikes was dramatic. After the first strike, the whale seemed unperturbed. After the second, it appeared, from its trumpet blowing and stationary position, to be annoyed but passive. After the third, it reacted with great intensity and subsequently appeared exhausted.

Based on these observations we conclude that adverse responses to rapidly repeated or prolonged noxious stimuli in whales may be incorrectly modeled as a linear function. Given the lack of any detectable response to the biopsy procedure in some animals, there seems to be a threshold for stressor amplitude below which no response will occur. Further, this threshold of tolerance may be dependent upon the specific activity in which the animal is engaged immediately prior to the time the stressor is applied; e.g., in our study animals engaged in feeding were unlikely to react to the strike of a biopsy dart. There likely are also individual differences in this threshold, as suggested by the wide variation in reactions observed.

Moreover, although one evidently can expect a graded response in the disturbance of the animal above its tolerance threshold, such gradation might be better modeled as an exponentially increasing stimulus-response function. As such, continuous or rapidly repeated moderate-level noxious stimulation could potentially lead to a general somatic alarm reaction, with endocrinologic consequences (Selye 1936, 1946). Thus, one of the important implications of this study for current management strategies to promote the recovery of endangered whale populations is that uncontrolled increases in the level or frequency of noxious intrusion into cetacean habitat may, suddenly and unexpectedly, have serious deleterious effects.

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Spatial and temporal distribution of juvenile Atlantic cod *Gadus morhua* in the Georges Bank-Southern New England region

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Abstract.–Commercial landings data and research-vessel survey data collected by the Northeast Fisheries Science Center during 1982–86 were analyzed to identify spatial and temporal patterns as well as possible mechanisms associated with juvenile cod *Gadus morhua* distribution. Analysis of survey data indicated that cod ages 1–2, age 3, and age 4+ were distributed at different depths during the spring; however, during the autumn, age-3 fish co-occurred with age 1–2 fish.

Analysis of commercial landings data revealed the following patterns of distribution for age-2 cod: In quarter 1, concentrations appeared in the Nantucket Shoals region and the central portion of Georges Bank; in quarter 2, the concentration was northeast of Nantucket Shoals and also remained on Georges Bank; in quarter 3, both aggregations moved northeastward into deeper waters, along the 100 m contour of the Great South Channel and the Northern Edge, respectively; and in quarter 4, the Nantucket Shoals concentration had moved southwestward to shallower water, resuming locations identified in quarter 1, while the Georges Bank concentration remained as in quarter 3.

While intraseasonal spatial distributions did not appear to be defined by temperature, seasonal shifts in concentration of juvenile cod were most likely associated with temperature.

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The Atlantic cod *Gadus morhua* has accounted for more catch, by weight, than any other species in the U.S. Atlantic coast groundfish fishery during the past two decades (Serchuk and Wigley In press). Recent declines in annual landings of cod from the Georges Bank–Southern New England region (N. Atl. Fish. Org. Div. 5Z) have generated concern for the fishery. Total nominal catches (U.S. and Canadian commercial landings, plus U.S. recreational catch) from this area dropped from a high of 64,000 metric tons (t) live weight in 1982, to 27,900 t in 1986. Although catches increased to 33,700 t in 1987, 64% of the catch in numbers and 36% in weight consisted of age-2 fish from the strong 1985 year-class (NEFSC 1988). Of the various commercial market categories of cod, 'scrod' generally represents the smallest size grouping of cod landed. Scrod landings paralleled the general decline of Georges Bank cod landings, decreasing from 8100 t in 1982 to 3400 t in 1986. In addition, Northeast Fisheries Science Center (NEFSC) research-vessel survey abundance indices for spring and autumn 1987 were among the lowest observed for cod in the 25-year survey time-series (Serchuk and Wigley In press).

During the period December 1986–March 1987, anomalously high discard rates of juvenile cod below the legal minimum landed size of 19 inches (48.3 cm) TL were associated with commercial trawling operations using small mesh in the Nantucket Shoals area. This high discard level led to an emergency action extending large mesh regulation (5.5-inch mesh in codend) to this region during 23 February–31 March 1988 to "reduce fishing effort and mortality on juvenile Atlantic cod stocks found in high concentrations in this area at this time" (Federal Register, 50 CFR Part 651, 26 Feb. 1988). Large mesh regulation was permanently extended to the Nantucket Shoals area in January 1989 (Federal Register, 50 CFR Part 651, 31 Jan. 1989) (Fig. 1). In addition, the "Nantucket Shoals scrod slaughter" may have prompted the development and implementation of the Flexible Area Action System (FAAS) by the New England Fishery Management Council (NEFMC) and the National Marine Fisheries Service (NMFS). Under this plan, the Regional Director, NMFS Northeast Region, could close an area to fishing, impose mesh size restrictions, or establish catch limits for a period of 3 weeks to 6 months to minimize discards of juvenile fish. This represents a significant departure from the traditional uses of seasonal or areal closures, such as protection of adult haddock *Melanogrammus aeglefinus* during spawning (Halliday 1987).

For such a plan to be effective, knowledge of fish distribution pat-

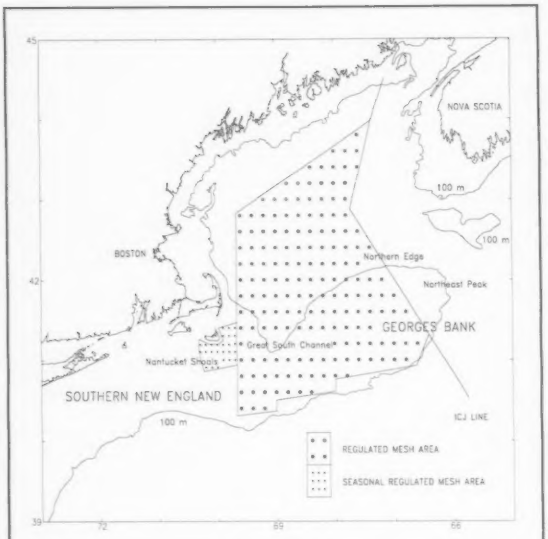

Figure 1
Georges Bank–Southern New England region of the Northwest Atlantic Ocean, showing geographic features and regulated mesh (5.5-inch) areas under the Northeast Multispecies Fishery Management Plan of the New England Fishery Management Council.

terns is necessary. In addition to documenting geographic, seasonal, and age-specific aspects of distribution, studies must examine mechanisms (such as temperature, depth, spawning, or feeding behavior) underlying these observed patterns. Numerous tagging studies have been conducted for Atlantic cod in the Northwest Atlantic: McKenzie (1934, 1956) and McCracken (1956) described cod movements in Canadian waters based on tagging experiments, and Smith (1902), Schroeder (1928, 1930), and Wise (1958, 1962) tagged cod from Woods Hole, Nantucket Shoals, and Nova Scotia to New Jersey, respectively. More recently, cod distributions delineated by bottom-trawl survey data from research vessels have been presented by Scott (1988) for Canadian waters and Grosslein and Azarovitz (1982) and Almeida et al. (1984) for U.S. waters. None of these studies considered fish size in the analyses. Overholtz (1984) found age-specific patterns of distribution for another gadoid species, haddock, in the Georges Bank region. Wigley and Gabriel (1991) and Bowman et al. (1987) examined distributions of several juvenile fishes, including cod, using NEFSC bottom-trawl survey data collected from Cape Hatteras, NC to Nova Scotia, Canada.

In our study, NEFSC commercial landings data and research-vessel survey data collected during 1982–86 were analyzed to identify spatial and temporal patterns as well as possible mechanisms associated with distributions of juvenile cod. The study period corresponds roughly to the duration of the NEFMC's Interim Fishery Management Plan for Atlantic Groundfish (31 March 1982 to 18 September 1986; NEFSC 1987). During this period, fishing practices were reasonably unchanged, although (1) an increase in minimum mesh size for the Georges Bank region from 5.125 inches (130 mm) to 5.5 inches (140 mm) was implemented on 1 April 1983, and (2) the International Court of Justice (ICJ) line dividing Georges Bank into U.S. and Canadian portions (Fig. 1) was established in October 1984. The study period also encompasses years of both strong and weak recruitment as well as a 50% reduction in spawning-stock biomass, events that allow evaluation of resulting distributions over varying year-class strengths and stock sizes.

Materials and methods

Distribution by temperature and depth

Temperature and depth analyses were based upon data collected for Atlantic cod during NEFSC spring and autumn bottom-trawl surveys during 1982–86 in the Georges Bank–Southern New England region in depths of 9–366 m. The stratified-random survey design and the standardization of survey gear and methodology are described in detail by Grosslein (1969) and Azarovitz (1981). Water-column temperature profiles, including bottom temperature (recorded to 0.1°C), were obtained on approximately half the survey stations via expendable bathythermographs; depths (m) were recorded using research-vessel electronic depth-sounding equipment. All cod were measured (FL to nearest cm) and a subset sampled for age, growth, and maturity information. Otoliths were processed and age determinations obtained according to procedures described by Penttila (1988); maturity staging was performed using classification criteria outlined by Burnett et al. (1989).

Estimates of mean temperature and depth (weighted by number of fish in each tow), and associated standard errors and ranges, were calculated by age for each season and tested for age-specific effects. Based upon results from analyses of individual age-groups, ages 1 and 2 were combined as well as fish age 4 or greater. These age-groups, as well as age-3 fish, were then retested for age-group specific effects. Assumptions of data normality were complicated by two factors. The first is the inherent nature of survey catch data as described by Pennington and Grosslein (1978), who found that the two most likely models for the distribution of fish (i.e., heterogeneous Poisson and randomly-

distributed clumps) both generated a negative binomial distribution. The second factor is that cod are not fully recruited to the survey sampling gear until age 3 or 4 (Serchuk and Wigley 1986). For these reasons, a distribution-free analysis of variance (Kruskal and Wallis 1952) was employed for statistical comparisons of temperature and depth distributions by age groups.

Spatial and temporal distribution

Commercial landings data (see Burns et al. [1983] for a detailed explanation of the commercial catch sampling program in the northeastern United States) for scrod cod collected by NEFSC during 1982–86 from the Georges Bank–Southern New England region (NEFSC Statistical Areas 521–526 and 537–539) were examined for spatial and temporal aspects of juvenile cod occurrences. Biases associated with the use of landings data were assumed to be negligible for this highly-directed fishery. Otter trawl catches account for 86–90% of the annual total cod landings (Serchuk and Wigley 1986); hence other gear types were excluded from subsequent analysis.

Table 1

Mean lengths-at-age, sample sizes, standard errors (SE), and range of observed values for age 0–10 cod *Gadus morhua* collected during NEFSC spring and autumn bottom-trawl surveys, 1982–86, in the Georges Bank–Southern New England region.

			Length (cm)		
Season	Age	N	$\bar{x}$	SE	Range
Spring	1	106	24.2	0.565	13.0–46.0
	2	458	43.8	0.253	26.0–58.0
	3	349	59.5	0.398	34.0–75.0
	4	212	69.0	0.570	46.0–89.0
	5	170	77.1	0.666	51.0–96.0
	6	69	84.7	1.013	64.0–108.0
	7	41	93.2	1.338	76.0–110.0
	8	24	102.5	2.235	79.0–124.0
	9	15	104.9	2.439	92.0–127.0
	10	5	102.8	5.678	87.0–119.0
Autumn	0	99	11.7	0.400	6.0–25.0
	1	279	36.9	0.308	23.0–51.0
	2	306	53.7	0.313	32.0–71.0
	3	145	68.0	0.557	42.0–83.0
	4	37	74.3	1.373	49.0–89.0
	5	16	85.4	2.432	60.0–99.0
	6	7	90.3	3.227	80.0–102.0
	7	6	98.8	2.613	94.0–110.0
	8	4	96.3	4.608	86.0–105.0
	9	3	105.0	5.196	96.0–114.0
	10	1	118.0	—	—

Fish in the scrod market category weigh 0.7–1.4 kg, measure 40–60 cm TL, and are 1–3 yr of age according to the growth function developed by Penttila and Gifford (1976).

Geographic resolution within Statistical Areas (SAR) was obtained by assigning the landings within each SAR to 10-min squares of latitude and longitude (~100 nm^2) based upon information from interviewed (i.e., dockside interviews of captains in which precise catch-location information was obtained) trips landing scrod cod. Scrod landings associated with interviewed trips were prorated upward for each 10-min square by the ratio, derived for each SAR, of total monthly landings to monthly interviewed landings. Prorated scrod landings were summarized quarterly for each year for each 10-min square.

Scrod cod landings were partitioned into age-groups 1, 2, 3 and 4+ by constructing a catch-at-age matrix using a technique described by Serchuk and Wigley (1986). In this method, quarterly mean weights for scrod cod were calculated by applying a length-weight equation to quarterly scrod length-frequency data; these means, in turn, were divided into scrod landings for the corresponding quarter to generate numbers landed. Age compositions for scrod landings were derived by applying quarterly age/length keys to numbers at length landed; resulting proportions at age were then applied to prorated scrod landings for each 10-min square to obtain estimates of landings by weight for each age-group.

Results

Temperature and depth distribution

Analyses of survey data were based upon 1455 and 904 cod collected during spring and autumn bottom-trawl surveys, respectively, during 1982–86. Mean lengths-at-age and associated statistics for cod ages 0–10 are presented in Table 1. Geographically, juvenile cod (defined as fish <37 cm, the minimum size at first maturity; Morse 1979) exhibited seasonal patterns of distribution. In spring, juveniles are dispersed throughout the Georges Bank–Southern New England region (Fig. 2A), while in autumn they are concentrated along the 100 m contour west of the Great South Channel and the Northern Edge and Northeast Peak of Georges Bank (Fig. 2B).

Differences in distribution with respect to both mean temperature and depth were noted for all age-groups of cod (Table 2). Mean temperatures were approximately 5.3°C in spring and 9.2°C in autumn for all age-groups, despite the fact that there was considerable overlap in the temperatures for the two seasons (Table 2). However, within seasons, differences in mean

temperature observed between age-groups were within 0.5°C, except for age-0 cod in the autumn (Table 2). In general, distribution patterns were delineated more by differences in depth than temperature.

No age-0 cod were captured during spring surveys due to their pelagic larval existence at this time (early April–early May). Age-1 and age-2 cod were found at significantly shallower mean depths than age-3 and age 4+ cod (57.0 and 58.0 m vs. 68.4 and 86.3 m, respectively; Table 2). The difference between mean depths of age-3 and age 4+ cod was also significant (Kruskal-Wallis ANOVA, $p<0.01$; Table 3). In the autumn surveys (corresponding to late September–late October), age-3 cod were observed at a mean depth similar to those for ages 1–2 (85.8 m vs. 86.8 and 85.2 m, respectively; Table 2) and significantly different (Kruskal-Wallis ANOVA, $p<0.01$; Table 3) from that for age 4+ cod (116.0 m; Table 2). Additionally, age-0 cod were captured in the autumn and observed to be distinct from all other age-groups with respect to both temperature and depth (Table 2).

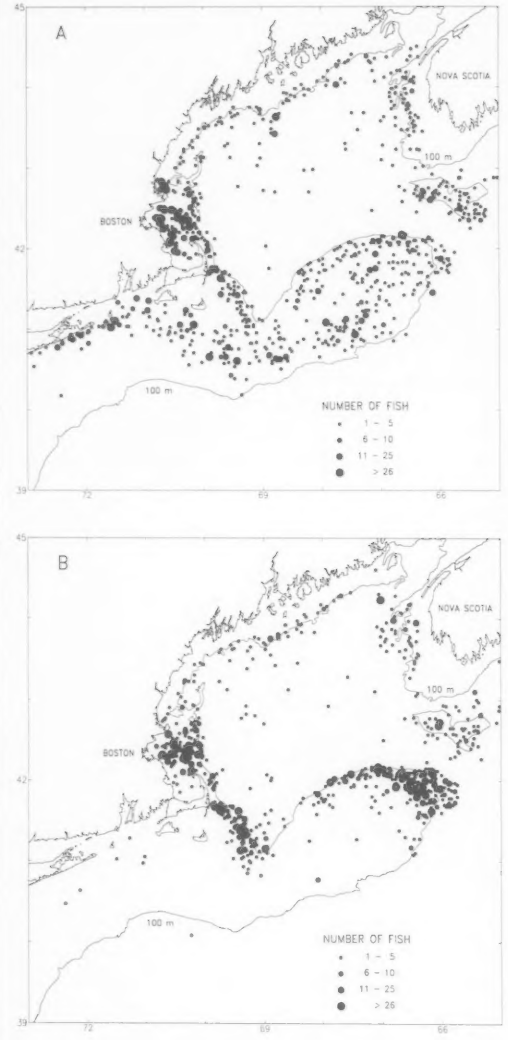

Figure 2
Geographic distribution (number/tow) of juvenile cod *Gadus morhua* <37 cm in length collected during NEFSC spring (A) and autumn (B) bottom-trawl surveys, 1968–86, in the Georges Bank–Southern New England region.

Spatial and temporal distribution

Statistical Area 521 accounted for 49% of total prorated scrod landings during the sampling period 1982–86, from a high of 57% in 1983 to a low of 29% in 1986, while SAR 523 and 522 contributed 14% and 13%, respectively; landings from Southern New England (SAR 537–539) accounted for only about 2% of total scrod landings (Table 4). Interviewed coverage was obtained for a high percentage of scrod landings

Table 2
Mean temperatures and depths, sample sizes, standard errors (SE), and range of observed values for age-groups 0, 1, 2, 3, and 4+ of cod *Gadus morhua* collected during NEFSC spring and autumn bottom-trawl surveys, 1982–86, in the Georges Bank–Southern New England region.

Season	Age	N	$\bar{x}$	SE	Range
			Temperature (°C)		
Spring	1	106	5.18	0.124	2.8–9.0
	2	458	5.03	0.050	3.3–12.1
	3	349	5.51	0.064	2.8–9.4
	4+	542	5.42	0.051	3.0–12.1
Autumn	0	99	10.02	0.233	5.8–14.3
	1	279	8.75	0.123	5.4–14.3
	2	306	9.02	0.108	5.4–14.3
	3	145	9.33	0.195	5.2–19.2
	4+	75	9.33	0.292	5.1–15.3
			Depth (m)		
Spring	1	106	56.98	2.001	25–122
	2	458	57.97	1.307	24–237
	3	349	68.36	1.966	24–210
	4+	542	86.34	2.346	25–307
Autumn	0	99	68.77	2.934	28–153
	1	279	86.80	2.185	28–230
	2	306	85.19	2.618	28–230
	3	145	85.80	3.945	31–205
	4+	75	116.00	7.793	26–328

Table 3

Results of Kruskal-Wallis analyses of variance of age-specific cod *Gadus morhua* distribution by temperature and depth by season, based on data for cod collected during NEFSC bottom-trawl surveys, 1982–86, in the Georges Bank–Southern New England region. NS = not significant, $p>0.05$; **highly significant, $p<0.01$.

Season	Age-group	Temp.	Depth
Spring	3 vs. 4+	NS	**
	1–2 vs. 3	**	**
	1–2 vs. 4+	**	**
Autumn	3 vs. 4+	NS	**
	1–2 vs. 3	NS	NS
	1–2 vs. 4+	NS	**

Table 4

Scrod cod *Gadus morhua* landings (t, live weight) by Statistical Area and year, 1982–86, in the Georges Bank–Southern New England region. Percentages of NEFSC commercial scrod landings for which interviewed coverage was obtained are given in parentheses. (Statistical Areas are shown in Figs. 3A–3D.)

Area	1982	1983	1984	1985	1986
521	4564(76)	4350(76)	1396(81)	3033(93)	1022(87)
522	1025(71)	978(73)	415(75)	855(93)	476(84)
523	1215(83)	958(95)	766(91)	939(87)	365(96)
524	554(68)	411(92)	517(92)	568(92)	757(84)
525	240(66)	109(80)	150(77)	204(91)	118(83)
526	466(92)	665(76)	413(90)	743(95)	579(84)
537	76(68)	135(73)	103(76)	60(74)	168(50)
538	4(30)	7(59)	3(61)	5(20)	5(60)
539	10(28)	3(22)	1(30)	<1(27)	<1(14)
Total	8154(76)	7616(79)	3764(84)	6407(92)	3490(84)

(76–92% annually during the period; Table 4), suggesting that the proration procedure employed in this study accurately depicts the patterns of landings.

Age-2 cod dominated commercial landings of scrod in all years except 1984 and 1986, when age-3 fish comprised the majority (Table 5); this exception is due to weak 1982 and 1984 year-classes (Serchuk and Wigley In press). Age-1 fish are too small to be caught by the commercial gear until quarters 3 and 4; conversely, age 4+ fish grow out of the scrod market category and into the next market category after quarter 2 (Table 5). Based upon these observations, and the observation above from analysis of survey data that age-3 cod are seasonally segregated from ages 1–2, analysis of juvenile cod distribution from commercial data was confined to age-2 fish.

Table 5

Age composition by weight (t, live weight) of scrod cod *Gadus morhua* landings by quarter, 1982–86, in the Georges Bank–Southern New England region.

Year	Age-group	Quarter 1	2	3	4	Scrod total
1982	1	0	0	4	230	234
	2	417	1140	3141	1836	6534
	3	190	469	203	31	893
	4+	198	240	56	0	494
	Total	805	1849	3404	2097	8155
1983	1	0	0	16	61	77
	2	199	976	1554	1260	3989
	3	437	1170	965	502	3074
	4+	212	156	93	15	476
	Total	848	2302	2628	1838	7616
1984	1	0	0	1	78	79
	2	73	381	395	418	1266
	3	611	672	395	102	1780
	4+	236	182	185	33	636
	Total	920	1235	976	631	3762
1985	1	0	0	10	101	111
	2	304	1002	1813	1826	4945
	3	192	510	335	123	1160
	4+	96	46	43	6	191
	Total	592	1558	2201	2056	6407
1986	1	0	0	0	120	120
	2	162	467	193	249	1071
	3	948	850	289	52	2139
	4+	148	4	8	0	160
	Total	1258	1321	490	421	3490

The following patterns of age-2 juvenile cod distribution emerged. In quarter 1, juvenile cod were concentrated in the Nantucket Shoals region (south of the stepped portion of the boundary between SAR 521 and 526) as well as being dispersed generally across the shallower central portions of Georges Bank, primarily in SAR 522 and 524 (Fig. 3A). By quarter 2, the area concentration was north of Nantucket Shoals (in SAR 521), while on Georges Bank there continued to be a dispersed distribution as in quarter 1 (Fig. 3B). In quarter 3, the Nantucket Shoals concentration had moved northeastward within SAR 521 to deeper water along the 100 m contour of the west slope of the Great South Channel; similarly, juveniles on Georges Bank had formed concentrations along the 100 m contour in SAR 522 (the east slope of the Great South Channel) and 523 (the Northern Edge and Northeast Peak areas; Fig. 3C). By quarter 4, the Nantucket Shoals concentration had

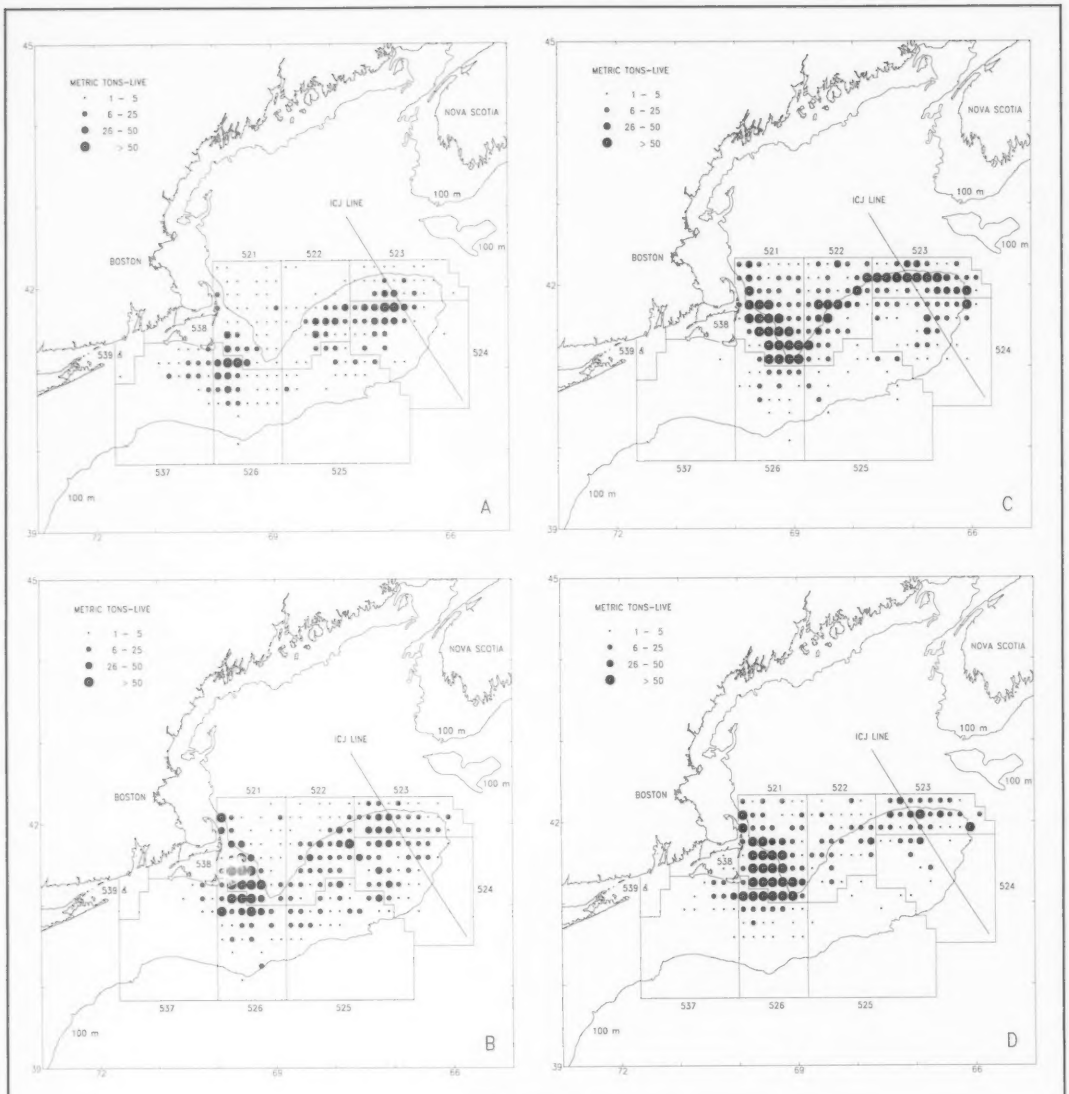

Figure 3

Distribution of age-2 cod *Gadus morhua* by 10-min squares of latitude and longitude from NEFSC scrod landings data (t, live weight), 1982–86, for quarters 1 (A), 2 (B), 3 (C), and 4 (D) in the Georges Bank–Southern New England region.

shifted south and southwestward within SAR 521 to shallower water and into SAR 526, resuming locations identified in quarter 1; however, the concentration on Georges Bank in SAR 523 was still present (Fig. 3D).

Visual inspection of quarterly distribution plots for each year suggested that these patterns of juvenile cod concentrations persisted over varying year-class strengths and stock sizes; however, in the interest of space, only aggregate plots are presented (Figs. 3A–3D). Age-2 cod from strong 1980 and 1983 year-classes (Serchuk and Wigley In press) exhibited the same seasonal movements described above, as did age-2 fish from the relatively weak 1982 and 1984 year-classes. Similarly, no changes in observed annual patterns were evident from 1982 to 1986, during which time spawning-stock biomass diminished from over 80,000 t to about 33,000 t (Serchuk and Wigley In press).

Discussion

The observed seasonal variation in distribution of age-3 cod relative to age groups 1–2 and 4+ may be associated with a transitional period involving both maturation and feeding habits. Age 3 encompasses a period in which there is a mismatch in size-at-first-maturity and the attainment of the adult diet. Median size and age at sexual maturity for cod is about 50 cm and 2.5 yr, respectively (Livingstone and Dery 1976), and during spring some age-3 fish recruit to the spawning population. Autumnal co-occurrence of age-3 fish with ages 1–2 may be related to diet. Bowman and Michaels (1984) presented data which indicate that cod <66–70 cm have not assumed the adult diet dominated by fish; the mean length of age-3 cod in autumn is 68.0 cm (Table 1).

In a mathematical evaluation of spatial distributions of several North Sea species, Houghton (1987) suggested that cod distributions were more complex and less persistent than those observed for haddock or flatfish. In this study, however, the spatial and temporal patterns observed for juvenile Atlantic cod from landings data were remarkably uniform over the study period, and did not seem to vary according to stock size or year-class strength. The use of commercial data in this study is somewhat constrained by management regulations, fishing practices, and the distribution of fishing effort, yet results from analysis of survey data in this study seem to corroborate these conclusions.

The use of mean values in this study to define patterns of temperature and depth distribution may better reflect general tendencies rather than absolute preferences; in actuality, cod of all ages except age 0 were found at virtually all available temperatures and depths. Yet the patterns that emerged in this study are, for the most part, consistent with those identified in other studies. Both Schroeder (1930) and Wise (1962) noted the tendency for older cod to move into greater depths. Scott (1988) found that cod in colder Canadian waters were distributed at temperatures of 2–10°C, with largest catches occurring at 4–6°C. The apparent contradiction posed by the movement of cod to deeper, warmer water in winter–spring observed by Scott (1988), and the observations in this study of movement to shallower water on Nantucket Shoals and Georges Bank during this period, is an artifact of the different temperature regimes for the two regions; in each case, cod are changing depth locations to maintain preferred temperatures. Schroeder (1930) reported cod occurrences within an annual range of 0–17°C in the region from Nantucket Shoals to North Carolina, and attributed the triggering of the autumn migration of Nantucket Shoals adult cod westward to New Jersey for winter spawning to falling bottom temperatures in October. Similarly, movements of juvenile cod from Nantucket Shoals to deeper water off Chatham and the Great South Channel in summer–early autumn were thought to be in response to locally-available, cooler temperatures (Schroeder 1930). Wise (1958, 1962) determined from tagging studies that a resident population of cod inhabited the Nantucket Shoals–Great South Channel area year-round, but that Nantucket Shoals also represented the summer residence for the population of cod that wintered off the coast of New Jersey. Thus, the distribution patterns observed in this study within SAR 521 and 526 would most likely reflect seasonal movements of resident cod, although the migratory population may partially contribute to landings for quarters 2 and 3 in SAR 526.

Scott (1982) concluded from an analysis of fish distribution by bottom type that, although generally associated with sand-gravel sediments, cod occurred over all substrates and that observed patterns of distribution were more likely due to the bottom-type preferences of major prey items (e.g., *Cancer* crabs, sand lance, *Ammodytes* sp., etc). Although no quantitative analysis of distribution by bottom sediment was undertaken here, the seasonal shifts in concentration identified in this study do not suggest any major change in substrate preference of cod. However, the Great South Channel and the Northern Edge–Northeast Peak regions, where concentrations of scrod cod occur in quarters 3 and 4, are characterized by coarser sediment types than those generally found elsewhere on Georges Bank (Wigley 1961, Schlee 1973).

Based on the above analyses, there is evidence for well-defined seasonal and geographic shifts in concentration for juvenile Atlantic cod in the Georges Bank–Southern New England region. Moreover, these patterns of concentration appear to be associated primarily with temperature. The high level of spatial and temporal resolution possible, i.e., 10-min squares of latitude and longitude and quarters, suggest that this type of study may be useful in assisting fisheries managers with decisions regarding seasonal and areal closures under the Flexible Area Action System.

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Larval development of two sympatric flounders, *Paralichthys adspersus* (Steindachner, 1867) and *Paralichthys microps* (Gunther, 1881) from the Bay of Coquimbo, Chile

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Abstract.–Developmental series of two sympatric flounders of the genus *Paralichthys*, found in the Bay of Coquimbo, are illustrated and described. The series consist of yolksac to metamorphosed larvae of artificially-reared *Paralichthys adspersus* (1.7–13.0 mm SL) and *P. microps* (1.5–11.0 mm SL). Field-collected larvae correspond to the size ranges found in reared larvae. Degree of cephalic spination (in particular, sphenotic spines), pigmentation pattern, and number of elongated dorsal-fin rays are useful for identification of yolksac-to-postflexion larvae of both species.

During early metamorphosis the most valuable characteristics for identification are the number of elongated dorsal-fin rays, although after their reabsorption several morphometric relationships have to be used. *Paralichthys adspersus* preflexion larvae have two sphenotic spines and almost no pigmentation in the dorsal finfold, while *P. microps* larvae have only one sphenotic spine and a well-pigmented dorsal finfold. Beginning at notochordal flexion, the number of elongated dorsal-fin rays, six for *P. microps* and three for *P. adspersus*, can be used to identify the larvae. During late metamorphosis, morphometric relationships of SnL/HL, HL/SL, and BD/SL must be used to identify the larvae. Flexion is complete at 7.2 mm SL and metamorphosis at ~11.0 mm SL in *P. microps*, and at 8.6 mm SL and 13.0 mm SL in *P. adspersus*, respectively.

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Paralichthys is one of the most important genera of flatfish on both coasts of North and South America (Ginsburg 1952), considering number of species, geographic distribution, and economic importance. Seven species of the genus have been reported in Chilean waters (Bahamonde and Pequeño 1975), *Paralichthys adspersus* (Steindachner 1867) and *P. microps* (Gunther 1881) being the most abundant and most widely distributed. The former is found from the coast of Paita (Peru) to Lota (Chile) and Juan Fernández Island; the latter from Huacho (Peru) to the austral tip of South America (Chirichigno 1974). Because these two morphologically-similar species co-occur over most of their distributional ranges, adult and larval identifications have been difficult. Muñoz et al. (1988) described larvae of *P. microps*, but recognized the possibility that specimens of both species were included in their sample. They indeed have one *P. adspersus* larva (3.2 mm, Fig. 2b). Silva (1988) published photographs of the eggs and some larvae of *P. microps*.

In this paper, taxonomic characters which separate these two species during early-life-history stages, from yolksac larva to juvenile, are described.

Material and methods

Most of the material examined in the present study was obtained from several experiments, resulting from artificial fertilization of eggs and sperm from ripe specimens captured in the Bay of Coquimbo (29°59′S).

Larvae were cultured in 200 L conical tanks, with a daily 25% water renewal. From hatching through flexion, larvae were fed the rotifer *Brachionus plicatilis* in concentrations of 5/mL, and from flexion through metamorphosis were fed *Artemia salina* nauplii in concentrations of 10/mL. Temperature range during the experiment was 13–17°C (Silva 1988). Larvae, sampled with a Bongo net (1 m, 500 μ mesh) and an epibenthic trawl (500 μ mesh) at stations in Coquimbo Bay and adjacent coastal areas, were compared with cultured larvae.

A total of 49 larvae of *P. adspersus* and 46 of *P. microps* were used; of these, 39 larvae of both species were cleared and stained using Potthoff's (1984) method to determine the sequence of development of the axial skeleton. Pterygiophores and rays were counted when present, regardless of their state of development. Larvae were anesthesized with MS-222 before fixing in 5% formalin, and were later preserved in 3% buffered formalin.

Specimens were divided into developmental stages following the definitions of Ahlstrom et al. (1976).

Table 1

Morphometric relationships in *Paralichthys adspersus* and *P. microps* larvae. *N* = number of specimens; measurements in mm; length = NL for preflexion–flexion stages, SL for postflexion–juvenile.

	Preflexion			Flexion		
Measure	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
Paralichthys adspersus						
N		21			11	
Length	5.52	1.12	(3.6–7.0)	7.80	0.55	(6.9–8.6)
PAL/SL	41.40	1.32	(40.5–43.5)	39.60	3.08	(31.9–42.0)
BD/SL	13.90	3.80	(13.0–18.1) 17*	22.80	5.08	(17.4–31.4)
BD†/SL						
HL/SL	18.20	1.13	(16.7–20.0)	21.50	2.53	(18.6–26.7)
UJL/HL	37.30	4.52	(29.4–39.4) 17*	37.90	2.32	(33.3–41.7)
LJL/HL	46.30	3.08	(41.2–51.8) 19*	48.10	3.15	(44.7–54.7)
SnL/HL	22.10	2.22	(18.3–26.8)	21.10	1.02	(18.9–22.4) 10*
ED/HL	28.00	2.36	(24.8–33.3)	26.80	1.50	(24.7–28.9)
Paralichthys microps						
N		22			8	
SL	4.17	0.95	(2.95–6.0)	6.86	0.35	(6.2–7.2)
PAL/SL	41.15	1.83	(38–44)	40.90	3.27	(35–45)
BD/SL	13.30	2.16	(10–18)	25.60	6.40	(19–37)
BD†/SL						
HL/SL	18.10	1.48	(15–20)	21.60	3.70	(17–28)
UJL/HL	34.60	3.60	(29–37) 11*	44.50	4.20	(38–50)
LJL/HL	51.98	4.50	(43–59) 20*	57.10	3.86	(50–62)
SnL/HL	22.90	3.56	(16–31) 20*	23.90	2.88	(20–28)
ED/HL	30.10	4.10	(23–43) 21*	26.80	1.70	(24–29)

	Postflexion			Metamorphosis			Juvenile		
Measure	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
Paralichthys adspersus									
N		7			6			4	
SL	8.90	0.35	(8.4–9.4)	10.00	0.53	(9.2–10.2)	13.60	1.04	(12.3–15.0)
PAL/SL	40.80	2.76	(37.6–45.2)	37.60	3.17	(33.9–43.5)	34.40	0.68	(33.3–35.0)
BD/SL	35.80	1.77	(33.7–38.2)	39.50	1.42	(36.6–41.3)	37.90	0.72	(37.2–39.0)
BD†/SL				41.90	2.90	(36.4–45.8)	35.30	0.83	(34.4–36.2)
HL/SL	30.60	2.35	(27.6–33.7) 6*	32.00	1.69	(29.7–34.7)	35.10	0.38	(34.7–35.7)
UJL/HL	34.10	1.71	(31.5–37.3)	34.50	1.49	(31.7–36.5)	34.40	0.94	(33.3–35.6)
LJL/HL	45.60	2.61	(41.7–50.5)	45.90	1.35	(42.9–48.4)	46.80	1.50	(44.4–48.1)
SnL/HL	20.70	2.55	(17.5–25.8)	18.30	1.66	(15.6–20.3) 5*	14.30	1.76	(11.5–16.3)
ED/HL	25.50	1.07	(24.1–26.8) 6*	25.00	2.57	(21.4–28.6)	28.70	2.09	(26.3–32.0)
Paralichthys microps									
N		4			8			4	
SL	6.90	0.77	(6–7.8)	9.30	0.67	(8.10–10.6)	15.20	1.95	(13.0–18.0)
PAL/SL	42.20	3.40	(37–46)	39.40	2.47	(36.2–43.5)	35.30	0.83	(34.4–36.2)
BD/SL	44.70	6.20	(35–46)	40.00	1.39	(37.7–42.0)	37.40	0.86	(36.2–38.5)
BD†/SL				46.50	1.03	(45.4–48.9)			
HL/SL	37.30	5.10	(32–46)	39.10	2.68	(35.8–43.0)	37.40	1.19	(36.3–39.4)
UJL/HL	38.90	2.10	(35–41)	37.80	2.09	(34.7–39.7) 6*	35.60	1.47	(34.3–38.0)
LJL/HL	50.70	4.30	(42–56)	47.90	2.70	(44.2–51.7) 6*	45.80	1.86	(43.1–46.9)
SnL/HL	23.20	1.90	(20–25)	23.30	1.73	(21.3–26.6) 6*	16.70	1.39	(15.5–19.0)
ED/HL	24.40	0.70	(23–25)	25.10	1.32	(23.0–26.6)	28.80	1.99	(25.4–30.2)

*N differs from number indicated above.

BD Body depth
BD† Body depth measured at anus
ED Eye diameter
HL Head length
LJL Lower jaw length
PAL Preanal length
SL Standard length
SnL Snout length
UJL Upper jaw length

Morphometric measurements follow the definitions of Gutherz (1970) and were made with an ocular micrometer (to 0.01 mm). Notochordal length (NL) was used for yolksac larvae through flexion: from then on, standard length (SL) was utilized. In preflexion and flexion larvae, body depth (BD) is defined as the vertical distance across the body at the anus including the dorsal-fin pterygiophores. After flexion, it is defined as the vertical distance across the body at the pelvic fin, from its base to the base of dorsal-fin rays. Head length (HL) is defined as the distance from the snout to the cleithrum, until and through flexion, and thereafter from snout to the opercle edge. The total number of myomeres and vertebrae does not include the urostyle. Drawings were made from a compound microscope equipped with a camera lucida.

Linear regression models were fitted to six morphometric relationships of the larvae, comparing the preflexion stages with flexion, postflexion, and metamorphosis, to separate larvae of both species. An F test (Neter and Wasserman 1974) was used to compare the morphometric relationships of these two groups of larvae within and between species.

Determination of *Paralichthys* adults was based on

Table 2

Osteological development sequence of fins in *Paralichthys adspersus* and *P. microps* larvae. Length = NL preflexion, SL postflexion.

	Paralichthys adspersus						*Paralichthys microps*					
	Rays + Pterygiophores		Rays + Radials		Rays		Rays + Pterygiophores		Rays + Radials		Rays	
SL	Dorsal	Anal	Pelvic	Pectoral	Caudal	Vertebrae	Dorsal	Anal	Pelvic	Pectoral	Caudal	Vertebrae
4.1							–	–	–	–	–	–
4.5							–	–	–	–	–	–
4.7	–	–	–	–	–	–						
4.8	–	–	–	–	–	–						
5.4	–	–	–	–	–	–						
5.5							0+1	–	–	–	–	–
5.9							0+2	–	–	–	–	–
6.1		–	–	–	–	–	2+2	–	–	–	–	–
6.2							3+3	–	–	–	–	–
6.2							3+3	–	–	–	–	–
6.5							3+4	–	–	–	–	3
6.5							4+5	0+20	–	–	–	27+–
6.7	2+3	–	–	–	–	–						
6.9	3+3	–	–	–	–	–						
7.0							9+60	24+49	–		6+7	29+–
7.1							64+62	53+51	3+0		8+7	30+–
7.2							69+68	?+53	5+0		1+9+8+1	34
7.7	3+3	–	–	–	–	9	71+69	57+55	5+0		1+10+8+1	34
7.7	3+4	–	–	–	–	26						
7.8							71+71	53+53	5+0		1+10+9+0	34
8.1	5+4	–	–	–	–	32	73+72	57+54	6+0		0+10+8+0	34
8.1	6+30	0+23	–	–	–	33						
8.1	10+60	0+48	–	–	–	33						
8.2	13+48	0+42	–	–	9+8	33						
8.5	45+64	38+51	3+0	–	9+9	33						
8.6	56+65	30+51	3+0	–	1+9+8+1	33	73+73	58+57	6+0	–	1+9+9+1	34
8.6	64+66	50+51	4+0	–	1+9+8+1	33						
8.6	69+67	55+53	5+0	–	1+9+8+1	33						
8.8	73+72	55+55	5+0	–	1+10+9+1	33						
9.2	71+71	57+57	5+0	–	1+9+9+1	32	75+75	60+59	6+0	0+2	1+10+8+1	34
9.7				–			75+75	64+61	6+0	3+0	1+10+8+1	35
10.1	74+72	59+57	6+0	–	1+9+9+1	34	72+71	58+56	6+2	6+3	1+10+9+1	33
10.2	70+70	54+53	6+0	0+3	1+9+9+1	33						
10.9	71+70	57+55	6+2	7+4	1+9+9+1	33						
11.3							70+68	59+57	6+3	14+4	1+9+9+1	34
12.3	68+66	55+54	6+3	14+4	1+10+9+1	33						
12.7							73+72	59+56	6+3	14+4	1+9+9+1	33
14.0	70+69	57+56	6+3	13+4	1+9+8+1	33						

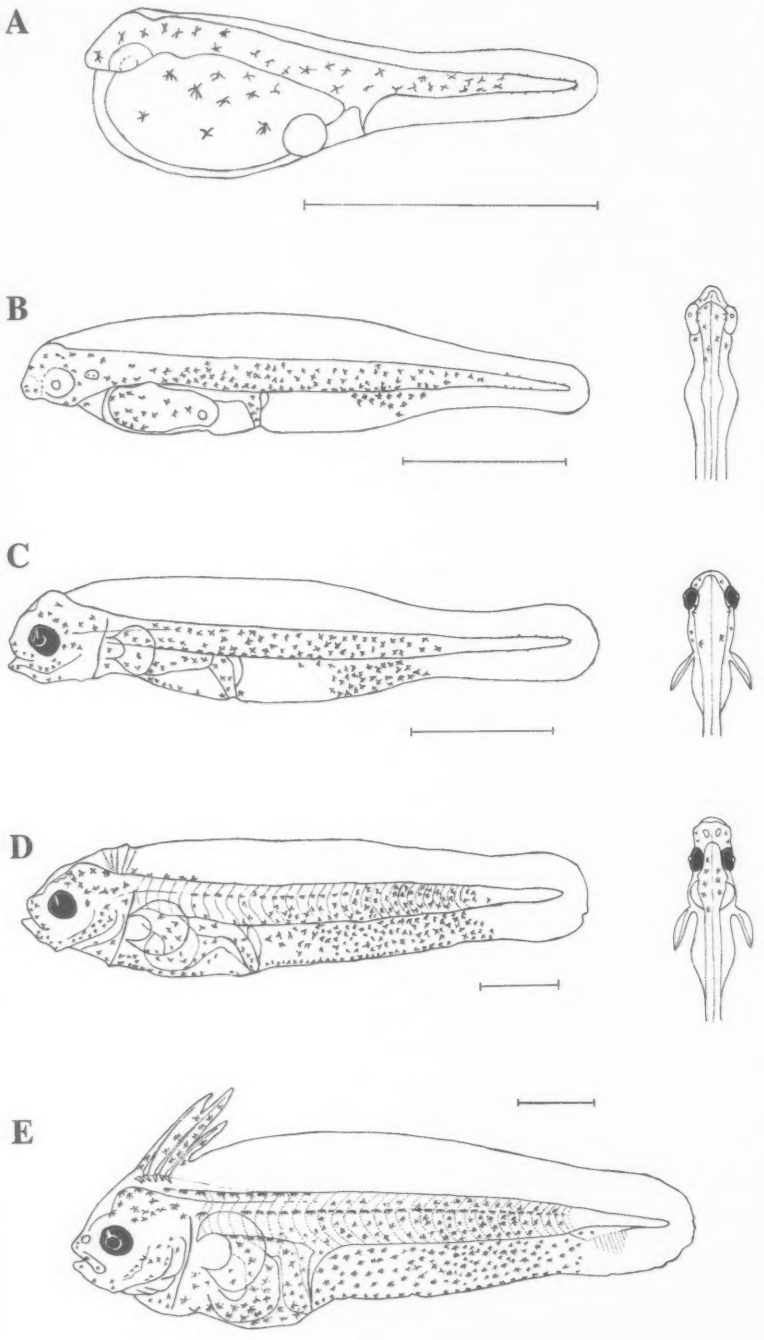

Figure 1

Paralichthys adspersus larvae. (A) Early yolksac, 1.7 mm NL; (B) late yolksac, 3.4 mm NL; (C) early preflexion, 3.9 mm NL; (D) late preflexion, 6.8 mm NL; (E) flexion, 7.7 mm NL. Drawings at right are dorsal head views.

the criteria of Ginsburg (1952), who observed that the origin of the dorsal fin in *P. microps* was over the center of the upper eye, while in *P. adspersus* it was over the eye's anterior margin. Furthermore, the number of gill rakers over the lower portion of the first arch is larger in *P. microps* (18–23) than in *P. adspersus* (15–19). An additional criterion found by Zuñiga (1988) referring to the size of the nostrils was also used.

Description

Paralichthys adspersus

Hatching occurs ~60 hours after fertilization. Larvae are ~1.7 mm NL; yolksac is more than half the body length; a small oil globule (0.13 mm) is present posterior to the yolksac (Fig. 1A).

Diagnosis The most important distinguishing features of preflexion *P. adspersus* larvae are the presence of two sphenotic spines (Fig. 2) and the lack of pigmentation in the dorsal finfold (Fig. 1). This last character may be useful through postflexion. Starting at notochord flexion, the presence of two groups of numerous opercular and preopercular spines, as well as 2–3 elongated dorsal-fin rays, is diagnostic. This last feature is useful until metamorphosis. Beyond metamorphosis, diagnosis should be based mostly on morphometric relationships.

Pigmentation Eyes of yolksac larvae are not pigmented. Few, relatively-large melanophores are found on the head, trunk, and yolksac except at the ventral margin (Fig. 1A). A series of small melanophores is present near the tip of the notochord. Pigment forms

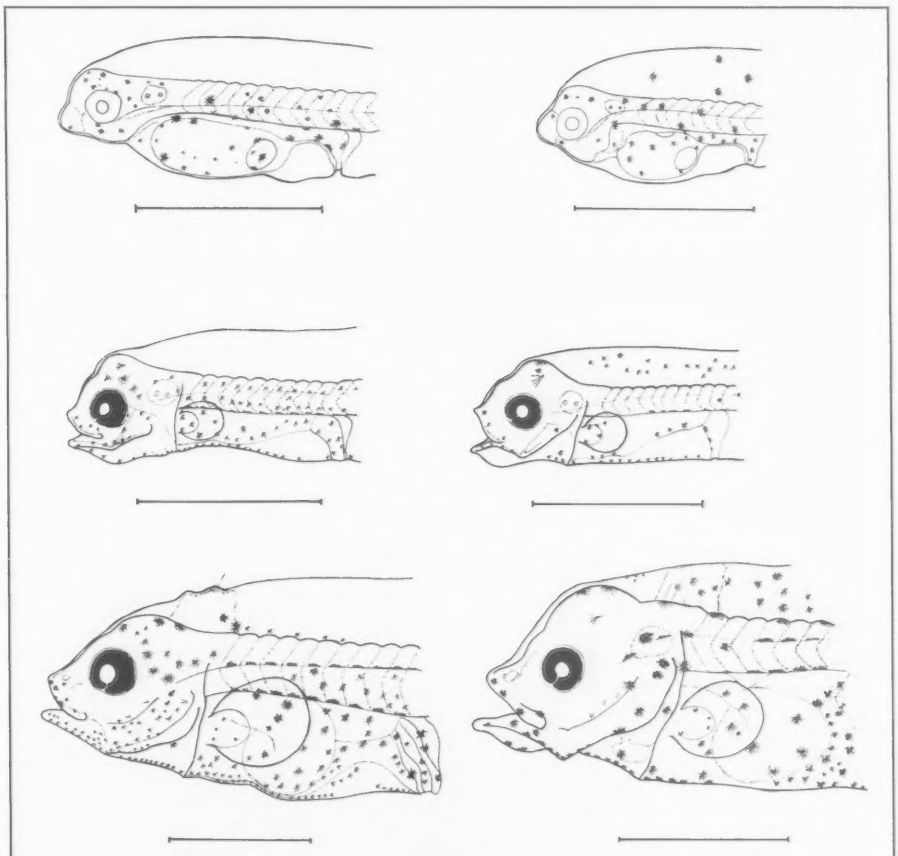

Figure 2
Heads of *Paralichthys adspersus* (left) and *P. microps* (right) larvae, showing number, size, and location of sphenotic, preopercular, and opercular head spines. Bars = 1.0 mm.

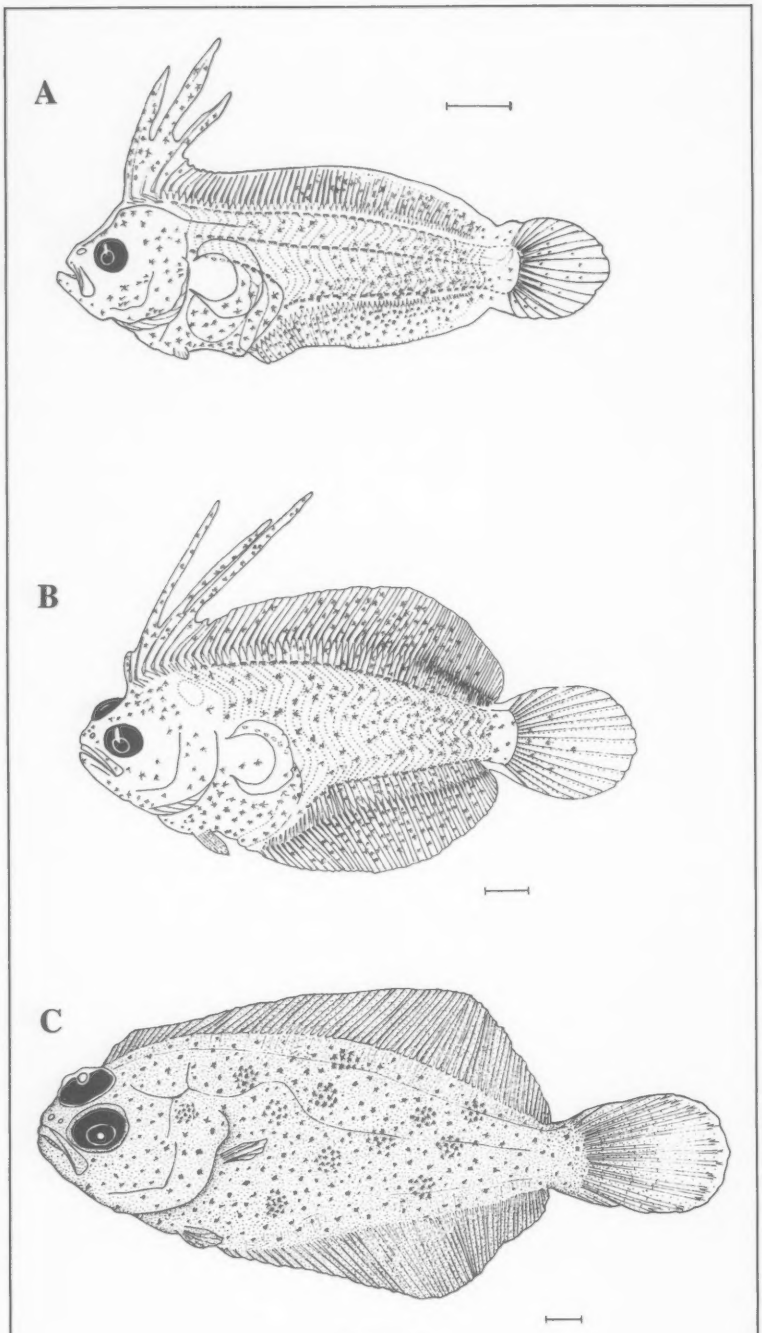

Figure 3
Paralichthys adspersus larvae. (A) Early postflexion, 8.8 mm SL; (B) early metamorphosis, 10.3 mm SL; (C) juvenile, 14.3 mm SL. Bars = 1.0 mm.

on the medial region of the pelvic fin. At the end of the stage (Fig. 1B), the eyes start to pigment.

During the preflexion stage (Fig. 1C, D), stellate melanophores are present on the head and over the anterior 2/3 of the body. Melanophores are absent on the dorsal finfold. At 3.5 mm NL, a series of melanophores forms on each side, slightly dorsal to the midline. At 4.0 mm NL, an embedded series of melanophores begins to develop dorsal to the notochord. A series of melanophores is present at the ventral margin of the body, from the gular region to the anus.

Head pigmentation consists of melanophores over both jaws, preopercle, opercle, and dorsal and lateral brain region. At about 5.0 mm NL, a melanophore is found internally above the palate, where it persists until metamorphosis.

At the beginning of the flexion stage (Fig. 3A), pigment intensifies in the tail region. The dorsal finfold generally remains unpigmented; however, a few melanophores appear in some specimens. A paired series of melanophores develops above the dorsum. Tail melanophores concentrate in the ventrolateral region, while the paired series dorsal to the notochord is less visible. The paired series dorsal to the gut becomes continuous with the gular–abdominal series. Head pigmentation increases. The interradial membrane of the elongated dorsal-fin rays becomes pigmented. Melanophores near the tip of the notochord persist but migrate as the caudal fin develops.

During postflexion (Fig. 3B), the melanistic pattern is similar to the previous stage except the paired dorsal series is more evident. The dorsal fin is pigmented, particularly in the posterior half, and the ventral region of the abdomen becomes pigmented.

During metamorphosis (Fig. 3C) pigmentation increases, especially on the left side of the body. Dorsal-fin pigmentation is concentrated in the posterior half of the fin. Groups of melanophores are present on the interradial membrane of the anal fin. The pelvic fin is almost completely pigmented.

Fin development Dorsal-fin pterygiophores and rays begin to form simultaneously at ~6.5 mm NL, reaching their full complements at 8.8 mm SL (Table 2). The anal-fin pterygiophores appear in advance of their corresponding fin rays, at 8.1–8.6 mm NL. In both fins, development proceeds posteriad. The pelvic fin appears at 8.5 mm NL, and all six rays are present at 10.1 mm SL. The hypural complex develops between 8.1 and 8.6 mm NL. There are 18 caudal-fin rays, plus 2 procurrent rays.

Morphology With absorption of the yolk, the yolksac larva becomes slender; the gut, jaws, and pectoral fins develop; and two sphenotic spines begin to develop on each side of the head. At 3.5 mm NL (4–5 days posthatching), the yolk is exhausted, the mouth is functional, eyes are pigmented, and the pectoral fin is formed.

Two sphenotic spines appear at ~3.0 mm NL on each side of the head (Fig. 2); initially the upper one is the larger. Both spines are reabsorbed before development of elongated dorsal-fin rays, near the end of this stage. On some specimens, a third, smaller sphenotic spine can be found below the first two.

At about 4.5 mm NL, preopercular and opercular spines appear; the former are located along the posterior margin of the preoperculum and on the anterior preopercular ridge. Opercular spines are located at the upper portion of the bone and are more prominent than preopercular spines.

At ~6.5 mm NL, the elongated rays of the dorsal-fin crest begin to appear. Three rays (corresponding to the second, third, and fourth dorsal-fin rays of the adult) form the initial crest. At 6.2 mm NL the gut begins to coil. During preflexion, body depth is moderate (13.9% NL) and preanal distance is ~41.4% NL. These proportions remain relatively constant during later development (Table 1). There are 33 myomeres (11 preanal and 22 postanal) at the end of the stage.

The beginning of the flexion stage is characterized by an increase in body depth (22.8% NL) and development of the caudal fin. Preopercular spines are in two series in the upper and lower margins of the bone. Opercular spines are also in two groups: an upper group on the body of the operculum and a lower one along its margin. Elongated dorsal-fin rays remain, the middle one being the longest. At ~7.5 mm NL, the pelvic fins begin to form and, by the end of the stage, rays and pterygiophores of dorsal, anal and caudal fins are more evident.

Morphometric proportions are similar to those of the previous stage, except body depth which increases. A small increase in head length is also apparent (Table 1). There are 33 (9 preanal and 24 postanal) myomeres at the end of the stage.

During postflexion, body depth increases to 35.8% SL; head length reaches 30.6% SL (Table 1). Dorsal-crest fin rays increase in relative length; the second reaches 50% SL. The short dorsal-fin ray anterior to the crest begins to develop.

Preopercular and opercular spination increases in some specimens, but the spines begin to reabsorb at the end of the stage. The interocular region begins to change in preparation for eye migration. There are 33 (7–8 preanal and 25–26 postanal) myomeres at the end of the stage.

During metamorphosis, body depth continues to increase (39.0% SL), and snout length decreases (18.3% HL); however, other body proportions do not change substantially (Table 1). The second elongated dorsal-fin ray reaches its maximum length (~53.9% SL) before being reabsorbed. Migration of the right eye to the left side begins. Pectoral-fin rays form. Preopercular and opercular spines are lost, as are the elongated dorsal-fin rays. Eye migration is completed at ~13.0 mm. The smallest juvenile was 12.3 mm SL (Fig. 3C). There are 33 (4–6 preanal and 27–29 postanal) myomeres at the end of the stage.

Paralichthys microps

Hatching occurs 57–68 hours postfertilization; yolksac larvae are ~1.5 mm NL; one oil globule is present. Yolksac development is similar to *P. adspersus* yolksac larvae, except that melanophores form on the dorsal and anal finfold and a simple sphenotic spine begins to develop at yolk exhaustion (~3.2 mm NL, 4–5 days after hatching).

Diagnosis Distinguishing features of preflexion *P. microps* larvae are the presence of only one sphenotic spine (Fig. 2) and the dorsal finfold with pigmentation. After notochord flexion until metamorphosis, the most distinguishing feature is the presence of more than 3, and later 6, elongated dorsal-fin rays (Figs. 4E, 5). After reabsorption of these elongated rays, diagnosis is mostly based on morphometric relationships.

Pigmentation During the preflexion stage, the pigmentation pattern is similar to that of *P. adspersus*, but *P. microps* larvae have a different arrangement of body and finfold melanophores and less head pigment. Melanophores are relatively sparse over the trunk and

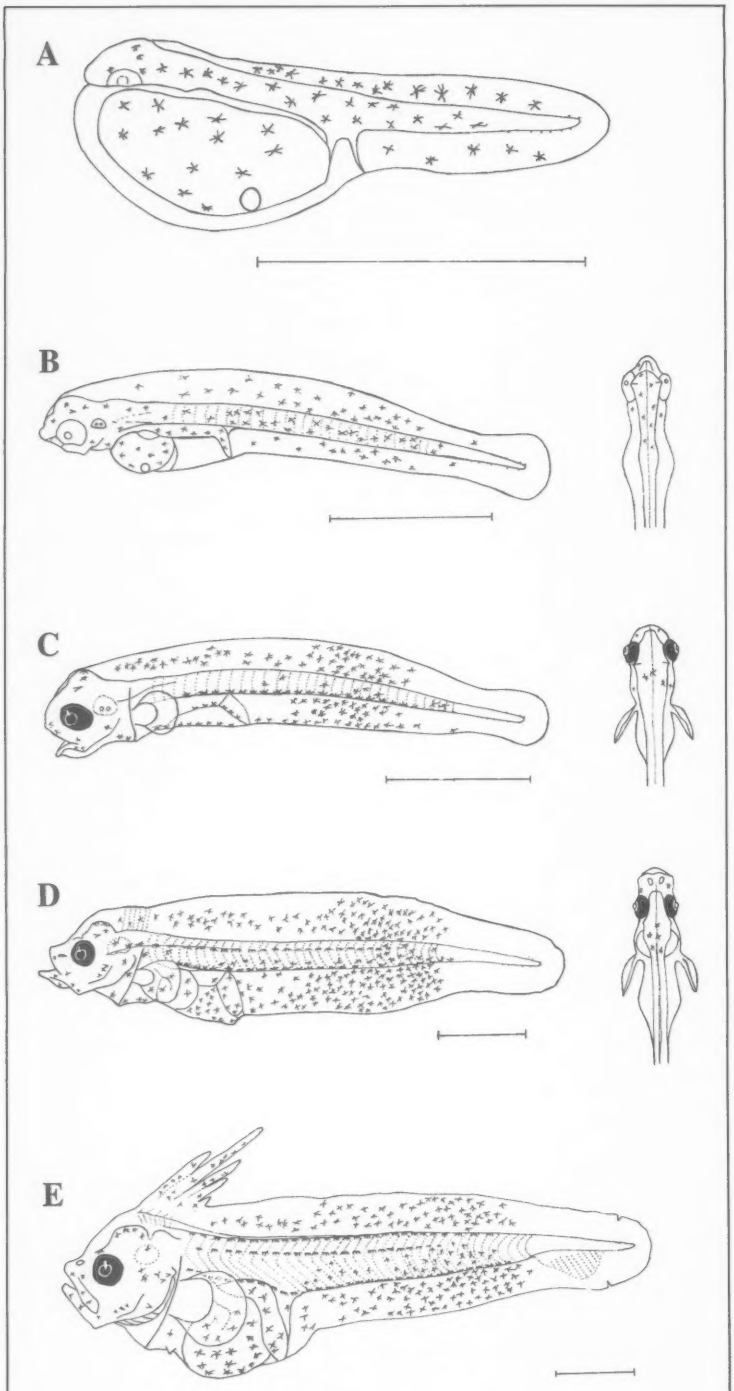

Figure 4

Paralichthys microps larvae: (A) Early yolksac, 1.5 mm NL; (B) late yolksac, 3.0 mm NL; (C) early preflexion, 3.4 mm NL; (D) middle preflexion, 5.3 mm NL; (E) late flexion, 7.0 mm NL. Drawings at right are dorsal head views. Bars = 1.0 mm.

anterior one-third of the tail. A dense zone of melanophores develops on the middle one-third of the tail and associated dorsal and ventral finfold regions (Fig. 4). Pigment is less dense on more anterior regions of the finfold and is absent on the posterior one-third of the tail and finfold. Head pigmentation is restricted to the jaws, dorsal brain, and opercle.

During the flexion stage, the melanistic zone on the tail and associated finfold region intensifies. The paired series along the dorsum and the epaxial region remains visible, while the embedded series dorsal to notochord is less visible due to the development of musculature. The number of ventral and ventrolateral abdominal melanophores increases. The ventral region of the gut has small melanophores, while those on the side of the gut are larger and stellate. The series above the gut and along its ventral midline are less apparent.

The pattern of melanophores on the head remains about the same, with brain melanophores the most conspicuous. Head pigmentation consists of small melanophores on the jaws, palate, preoperculum, operculum, and gular region, and larger and stellate melanophores in the brain region. The small melanophores located at the ventral margin near the tip of the notochord disappear with development of the caudal fin. Melanophores increase in number on the dorsal-fin crest and on the interradial membranes of the dorsal and anal fins during the postflexion stage (Fig. 5A).

Finally, during the metamorphosis stage (Fig. 5C) melanophores increase in numbers on the head and body, especially on the left side. Body melanophores are associated with myosepta. The paired dorsal series remains visible. Melanophores on the dorsal and anal fins are arranged in groups. The elongated dorsal-fin rays are covered with melanophores. The rear margins

of the hypural plates become pigmented, as do the bases of the caudal-fin rays.

Fin development Pterygiophores and fin rays of the dorsal fin appear at 5.5 mm NL; full complements are present at 7.7 mm SL (Table 2). Anal-fin pterygiophores and rays appear at 6.5 mm NL and have full complements at 7.7 mm SL. The pelvic-fin rays begin to develop at 7.0 mm NL and all are present at 8.1 mm SL; pterygiophores begin to develop at 10.1 mm SL and all are present at 11.3 mm SL. The first pectoral-fin rays appear at ~9.5 mm SL; full complements are present at 11.3 mm SL. The hypural complex develops between 6.2 and 7.2 mm NL. The number of caudal-fin rays is 18, plus 2 procurrent rays.

Morphology The sphenotic spine is more developed than in *P. adspersus* preflexion larvae (Fig. 2) (max. length is 24% eye diameter) and disappears with the appearance of the elongated dorsal-fin rays. At ~5 mm NL, up to 4 spines may be found at the preopercular margin; up to 3 spines are found in the upper region of opercle. At this size, the gut becomes coiled and the larva is moderately slender. Preanal distance is 41.2% NL; body depth (BD) is 13.3% NL, and upper jaw length (UJL) is 34.6% HL (Table 1).

At ~6 mm NL, three elongated rays appear on the dorsal fin crest. They correspond to the second, third, and fourth rays of the adult fin. The middle ray of the crest is the longest. There are 34 (11–12 preanal and 22–23 postanal) myomeres at the end of the stage.

The flexion stage is characterized by development of the hypural elements of the caudal fin. Body depth increases to 25.6%

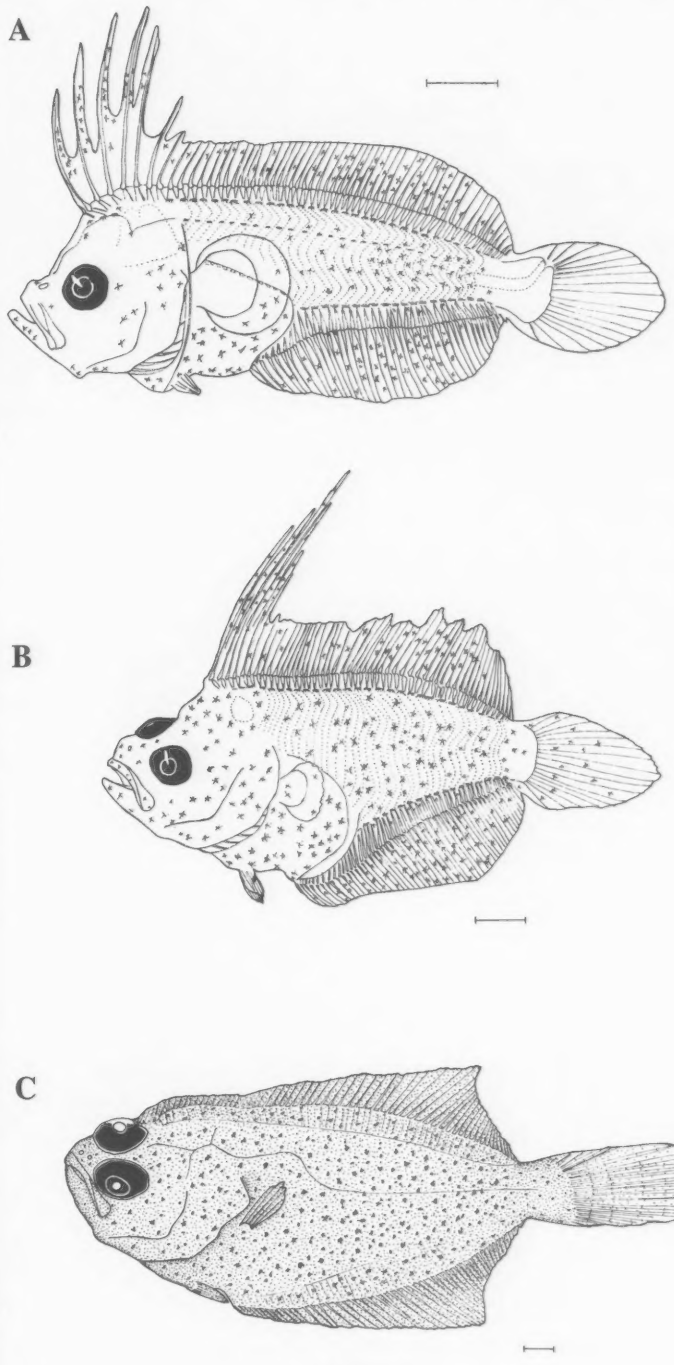

Figure 5
Paralichthys microps larvae. (A) early postflexion, 7.4 mm SL; (B) early to middle metamorphosis, 8.7 mm SL; (C) juvenile, 15.5 mm SL. Bars = 1.0 mm.

NL; upper and lower jaw lengths increase to 44.5% and 57.1% HL. Relative eye diameter decreases to 26.8% HL (Table 1).

The number and location of preopercular and opercular spines remain almost constant. The pelvic fin starts to develop at ~7.0 mm NL. Up to 6 elongated fin rays develop in the dorsal crest. There are 34 (9–11 preanal and 23–25 postanal) myomeres at the end of the stage.

The 6 (sometimes 7) fin rays of the dorsal crest continue to elongate during the postflexion stage. The fourth and fifth rays are more than half the body length; the first dorsal-fin ray is apparent but poorly developed. Rays and pterygiophores of median fins become more apparent.

By the end of this stage, preopercular and opercular spines start to disappear and the interocular region begins to deform in preparation for eye migration. Body depth increases (up to 44.7% SL) as does head length (up to 37% SL), with a corresponding decrease in relative jaw length and eye diameter (Table 1). There are 34 (7–9 preanal and 25–27 postanal) myomeres at the end of the stage.

Finally, during metamorphosis as the right eye migrates towards the left side of the body, the dorsal crest is lost, the mouth changes form, and pectoral-fin rays form (Fig. 5C).

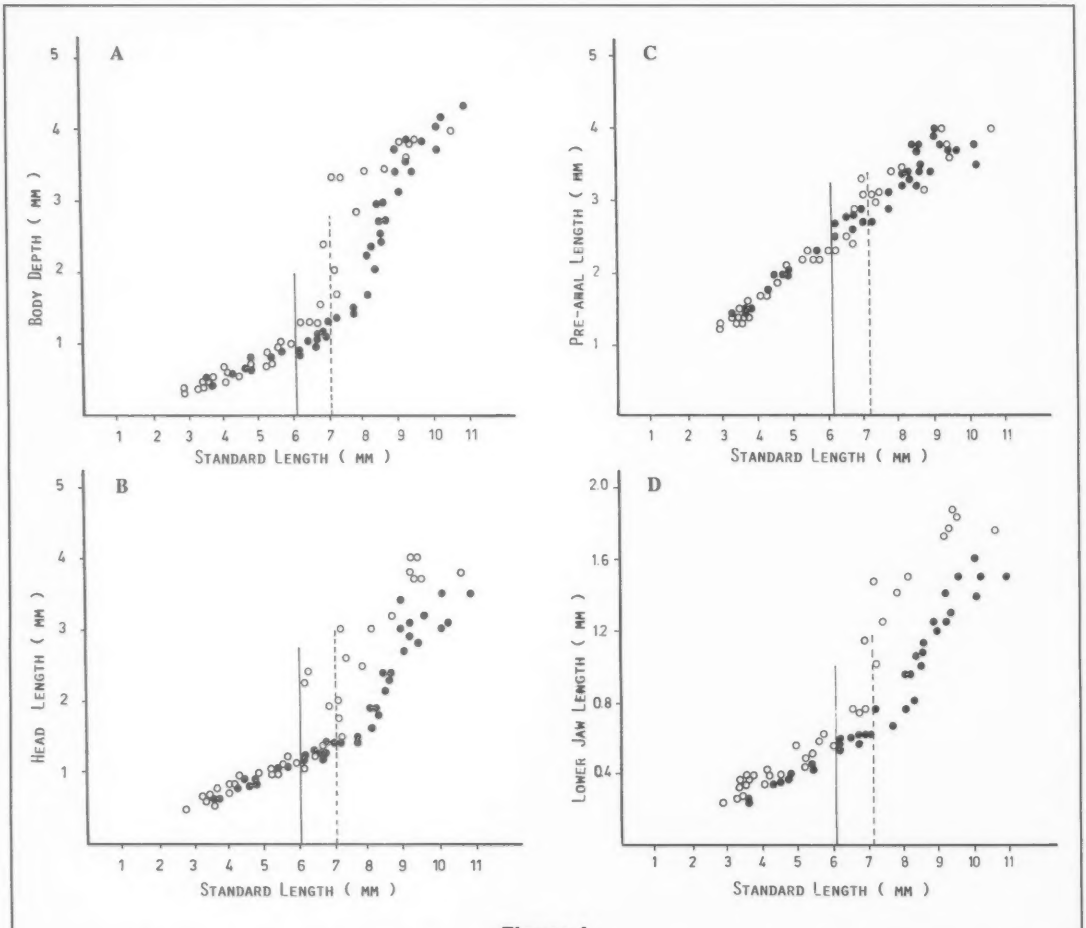

Figure 6

Morphometric relationships (vs. SL) of *Paralichthys adspersus* (●) and *P. microps* (○) larvae. (A) Body depth; (B) head length; (C) preanal length; (D) lower jaw length. Solid vertical line shows flexion of *P. microps*, and broken line flexion of *P. adspersus*.

Morphometrics

Six morphometric functional relationships are shown in Figures 6 and 7, and all linear regression models and their r^2 values are summarized in Table 3 (abbreviations as in Table 1). In general, all morphometric relationships were adequately described by the linear regression model, especially the preflexion *P. adspersus* larvae which always had higher r^2 values than those for other stages of the same species and all stages of *P. microps* (Table 3). The relationships are not so clear in *P. microps*, because the preflexion SnL/HL, PAL/SL, BD/SL, and HL/SL relationships had higher r^2 values than those of the other stages, while the relationships UJL/SL, LJL/SL, and ED/SL of other stages had higher values of r^2 than those from preflexion (Table 3).

F tests showed that models for all preflexion relationships and the PAL/SL of "other stages" could be considered statistically identical for both species, while all others were significantly different (Table 4). Regression models for all morphometric relationships (except SnL/HL and PAL/SL) between the two groups of developmental stages of *P. microps* were significantly different, while in *P. adspersus* all but SnL/HL, PAL/SL, and UJL/SL were significantly different (Table 5).

A summary of larval characters useful to identify larvae of both species during the different larval stages, including morphology, pigmentation, and morphometrics, is shown in Table 6.

Discussion

Characteristics of larval development of *P. adspersus* and *P. microps* are, in general, similar to those observed in other species of the genus (*P. dentatus* Smith and Fahay 1970; *P. olivaceus* Mito 1963, Okiyama 1967; *P. californicus*, Ahlstrom and Moser 1975). Important common characteristics are: presence of only one oil globule posteriad in the yolksac larvae; small size at hatching, notochordal flexion, and metamorphosis; presence of sphenotic spines; two groups of preopercular spines; elongated anterior dorsal-fin rays; a deep laterally-compressed body; and a large visceral mass. Opercular spines present in the two species described herein are uncommon in the family.

Length at hatching of Paralichthyid larvae varies between 1.5 and 3.7 mm NL with a mean of 2.2 mm, while the range described for the genus *Paralichthys* is 2.0–2.8 mm (Ahlstrom et al. 1984). Thus, hatching sizes (1.5–1.7 mm) of *P. adspersus* and *P. microps* larvae are smaller than any known congener. Lengths at flexion and metamorphosis of both species fall within

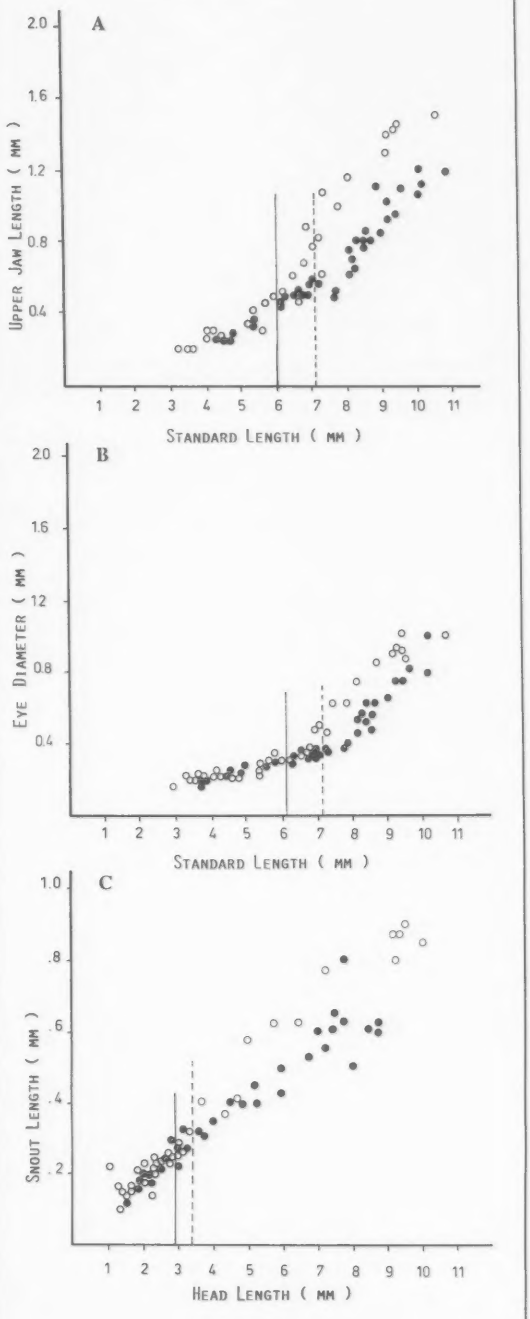

Figure 7
Morphometric relationships (vs. SL and HL) of *Paralichthys adspersus* (●) and *P. microps* (○) larvae. (A) Upper jaw length, (B) ocular diameter, (C) snout length. Symbols as in Fig. 6.

Table 3

Linear regression equations and r^2 values of selected morphometric relationships for preflexion and "other stages" larvae of *Paralichthys adspersus* and *P. microps*. Abbreviations as in Table 1.

	P. adspersus		*P. microps*	
Relationship	Preflexion	Other stages	Preflexion	Other stages
PAL/SL	0.091+0.397X r^2 0.975	0.652+0.328X r^2 0.557	0.088+0.388X r^2 0.957	0.534+0.338X r^2 0.772
BD/SL	−0.311+0.205X r^2 0.933	−5.446+0.944X r^2 0.873	0.328+0.214X r^2 0.901	−2.940+0.711X r^2 0.821
HL/SL	−0.189+0.218X r^2 0.971	−3.428+0.669X r^2 0.817	−0.149+0.217X r^2 0.937	−3.806+0.796X r^2 0.905
UJL/SL	−0.284+0.119X r^2 0.956	−1.012+0.215X r^2 0.701	−0.129+0.094X r^2 0.805	−1.060+0.258X r^2 0.889
LJL/SL	−0.137+0.110X r^2 0.974	−1.390+0.288X r^2 0.723	−0.034+0.104X r^2 0.815	−1.165+0.309X r^2 0.860
ED/SL	0.026+0.046X r^2 0.931	−1.114+0.199X r^2 0.911	0.047+0.042X r^2 0.785	−0.839+0.187X r^2 0.934
SnL/HL	−0.031+0.254X r^2 0.896	0.082+0.166X r^2 0.794	0.006+0.223X r^2 0.792	0.033+0.222X r^2 0.958

Table 4

Values of F for two regression models of morphometric relationships between preflexion and other developmental stages (flexion, postflexion, and metamorphosis) between *Paralichthys adspersus* and *P. microps*. Abbreviations as in Table 1.

	Preflexion			Other stages		
Relationship	F	df		F	df	
PAL/SL	1.18	(2, 41)	NS	0.05	(2, 38)	NS
BD/SL	0.66	(2, 38)	NS	11.24	(2, 38)	*
HL/SL	2.04	(2, 38)	NS	21.82	(2, 38)	*
UJL/SL	2.46	(2, 23)	NS	19.73	(2, 38)	*
LJL/SL	1.28	(2, 36)	NS	17.79	(2, 35)	*
ED/SL	0.67	(2, 38)	NS	34.97	(2, 33)	*
SnL/HL	1.25	(2, 38)	NS	14.81	(2, 35)	*

NS = Non-significant *Significant ($P<0.001$)

Table 5

F tests for two regression models of morphometric relationships between preflexion and other developmental stages (flexion, postflexion, and metamorphosis) within two species of *Paralichthys*. Abbreviations as in Table 1.

	P. adspersus			*P. microps*		
Relationship	F	df		F	df	
PAL/SL	0.79	(2, 43)	NS	1.48	(2, 36)	NS
BD/SL	50.90	(2, 41)	*	17.18	(2, 35)	*
HL/SL	22.90	(2, 41)	*	36.18	(2, 35)	*
UJL/SL	3.32	(2, 34)	NS	10.52	(2, 25)	*
LJL/SL	10.39	(2, 40)	*	18.03	(2, 35)	*
ED/SL	70.53	(2, 37)	*	51.96	(2, 34)	*
SnL/HL	2.14	(2, 40)	NS	0.83	(2, 33)	NS

NS = Non-significant *Significant ($P<0.001$)

the known range of the genus. *P. adspersus* is larger at metamorphosis than *P. microps* (9.6–13.0 mmSL vs. 8.0–11.0mmSL, respectively) and is comparable to the 10.2–14.2mmSL range for *P. olivaceus* (Okiyama 1967).

Early presence of elongated anterior dorsal-fin rays in *P. adspersus* and *P. microps*, at 6.5 and 6.0mmSL, respectively, is common in *Paralichthys* and related genera of paralichthyids (*sensu* Ahlstrom et al. 1984). The six elongated dorsal-fin rays observed in *P. microps* fall within the described range (4–8) for *Paralichthys*, while *P. adspersus* only has 3, as in the related genus *Citharichthys* (Ahlstrom et al. 1984). The shape and size of these dorsal-fin rays is characteristic of the genus *Paralichthys* and not *Citharichthys*.

The melanistic pattern of the larvae of both species is very similar to that described for the genera *Paralichthys* and *Pseudorhombus* (*sensu* Ahlstrom et al. 1984); however, the pigment series along the horizontal septum described for other species

Table 6

Summary of larval characters which distinguish larvae of *Paralichthys adspersus* and *P. microps* during different larval stages. Abbreviations as in Table 1.

Developmental stage	*P. adspersus*	*P. microps*
Preflexion	Two sphenotic spines present before development of dorsal-fin rays. Dorsal finfold unpigmented. LJL/HL = 46.3%	One sphenotic spine present before development of dorsal-fin rays. Dorsal finfold pigmented. LJL/HL = 52.0%
Flexion	Dorsal finfold unpigmented. LJL/HL = 48.1% 2–3 elongated dorsal-fin rays.	Dorsal finfold pigmented. LJL/HL = 57.1% 3–6 elongated dorsal-fin rays.
Postflexion	Dorsal fin poorly pigmented. HL/SL = 30.6%; BD/SL = 35.8% 3 elongated dorsal-fin rays. 33 myomeres.	Dorsal fin pigmented. HL/SL = 37.3%; BD/SL = 44.7% 6 elongated dorsal-fin rays. 34 myomeres.
Metamorphosis	3 elongated dorsal-fin rays (before reabsorption). SnL/HL = 18.3%; HL/SL = 32.0%; BD†/SL = 41.9% 33 myomeres.	6 elongated dorsal-fin rays (before reabsorption). SnL/HL = 23.3%; HL/SL = 39.1%; BD†/SL = 46.5% 34 myomeres.
Juvenile	33 vertebrae. Meristics (see Table 7).	34 vertebrae. Meristics (see Table 7).

BD† measured at the anus.

Table 7

Meristics of adult *Paralichthys adspersus* and *P. microps* of use in identifying juveniles.

Character Norman (1937)	*P. adspersus* Ginsburg (1952)	*P. microps*	
Origin of dorsal fin	Between anterior margin of eye and pupil (7–12 cm). Over anterior margin of eye or near it (20–39 cm).	Over or slightly anterior to center of eye.	
Gill rakers			
Upper	15–19	18–23	
Lower	7–8 ($\bar{x}$ 7)	9–10	Chirichigno (1974)
Total	22–27 ($\bar{x}$ 25–26)	27–33	
Fin rays			
Dorsal	68–76	68–80	
Anal	54–61	56–65	
Pectoral	11–13	11–12	

is not present in *P. adspersus* or *P. microps*. Reared and field-caught specimens of *P. adspersus* lack pigmentation in the dorsal finfold during the first half of their larval development, a unique feature among described paralichthyid larvae.

In flounders, the main change in body shape occurs during flexion, with an increase in body depth and head length. This stage is characterized by development of skeletal structures and by a change in swimming and feeding (Balart 1984). After flexion, the rate of growth of the head, snout, and jaws is comparatively greater in *P. microps*, while the rate of increase in body depth is greater in *P. adspersus*.

Preflexion larvae of *P. adspersus* and *P. microps* are statistically indistinguishable using morphometrics. After flexion and loss of the elongated dorsal-fin rays, separation is based mostly on morphometric characteristics, especially SnL/HL and HL/SL. After metamorphosis, during the juvenile stage when all fin rays are already developed, the adult range of meristic counts can be used (Table 7).

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An estimate of the tag-reporting rate of commercial shrimpers in two Texas bays

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Tag return rates are used to estimate exploitation rates for many animal species including penaeid shrimp. To avoid systematic underestimation of exploitation, the number of tagged animals recaptured but not reported must be reliably estimated (Paulik 1963, Youngs 1972, Seber 1973). Some investigators have offered rewards for tags to increase the tag return rate, but have incorrectly assumed that all or nearly all harvested tagged animals were reported (Kutkuhn 1966) or the rate of non-reporting remained the same throughout the experiment (Klima 1974, Kutkuhn 1966). Studies to measure the reporting rate of commercially-caught shrimp were conducted by Klima (1974) and Johnson (1981). The numbers of shrimp placed in both studies were small (n 71 and 20, respectively) and return rates differed markedly (82% and 10%, respectively). One drawback of these studies is that tagged shrimp were placed into the catch at shrimp houses or in the final processing stages, and not on the vessel during shrimping operations. Therefore, return rates during fishing operations were not measured.

Accurate reporting rates for recovered tags are essential for the determination of fishing mortality rates. The objective of the present study was to determine reporting rates of tagged shrimp captured during regular shrimping operations. To that end, tagged shrimp were surreptitiously placed in unculled catches. The reporting rates determined in this study are intended for use in correcting fishing-mortality estimates generated from a tagging program conducted during the same period.

Materials and methods

Texas Parks and Wildlife Department (TPWD) personnel placed tagged shrimp in the catch aboard Galveston and Aransas Bays' commercial bay and bait shrimp boats, May–November 1984. TPWD personnel and game wardens boarded shrimp vessels during bay shrimping operations. While a game warden distracted the crew by checking licenses, other TPWD personnel placed a single tagged shrimp in unculled catches (on deck) or in a live bait box. To conceal surreptitious placement of shrimp, 20 individuals of the target species *Penaeus aztecus* or *P. setiferus* were measured to the nearest mm total length (TL) on each vessel. A total of 219 shrimp (115 brown and 104 white) were surreptitiously placed aboard vessels in Aransas (n 125) and Galveston (n 94) Bay systems during the study period. No more than 12 shrimp were surreptitiously placed in each bay system in any one week.

Each tag was a uniquely-numbered black vinyl streamer (95 mm long × 4 mm wide) tapered at each end (Klima et al. 1987). Each tag was inserted between the second and third abdominal segments of the shrimp. Shrimp in Aransas Bay were measured (TL) prior to placement and after being returned by the fisherman. Since lengths were not required in the original study, measurements were not recorded in Galveston Bay. Lengths of shrimp placed in the catches and lengths of shrimp returned by fishermen were compared using student's t-test. Also, length frequencies of measured shrimp on commercial boats (n 2402) and of shrimp surreptitiously placed (n 105) aboard boats were compared visually using length-frequency histograms.

As part of a larger bay shrimp-tagging program conducted jointly by the TPWD and the National Marine Fisheries Service (NMFS), rewards were offered for tag returns. The program was promoted by distribution of posters to area shrimp dealers and through newspaper articles. No information was provided to the public concerning the surreptitious tagging activity.

Reporting rates (n reported/n placed, expressed as percent) were estimated for each species and bay system. Reporting rates and confidence intervals were estimated for the two bay systems combined. Reporting rates between species and between bay systems were compared using a Chi-square test (Sokal and Rohlf 1981).

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Results

Overall, 16% (95% CI, 11–21%) of 219 tagged shrimp were returned (Table 1). The return rate of 21% for brown shrimp was greater than the 11% for white shrimp (χ^2 4.415, 1df, $P \leq 0.05$). Reporting rates did not differ between bay systems for brown shrimp (χ^2 2.081, 1df, $P > 0.05$) or white shrimp (χ^2 1.059, 1df, $P > 0.05$). Reporting rates for the two species of shrimp were similar in Galveston Bay (χ^2 0.001, 1df, $P > 0.05$); in Aransas Bay, reporting rates were greater for brown shrimp (χ^2 6.890, 1df, $P \leq 0.05$). Sixty-eight percent of shrimp returned were reported found on the same day as placement.

Mean lengths of placed and returned brown shrimp from Aransas Bay were similar (t −0.48, $P > 0.05$) (Fig. 1), while the mean length of placed white shrimp was smaller than the mean length of those returned (t −4.01, $P \leq 0.05$). Placed brown shrimp were similar in length to those measured from the unculled catches on commercial shrimp boats (Fig. 2) whereas placed white shrimp were clearly smaller than those measured on commercial boats.

Discussion

Tag reporting rates for bay-caught shrimp have been reported by Klima (1974) and Johnson (1981). Tag reporting rates presented in this study are more precise because sample sizes were larger than in previous studies. Moreover, tag return rates in this study are more realistic because the tagged shrimp were placed in the catch before any processing occurred, rather than at dockside during the final processing stages.

The detection rate, and thus the reporting rate, of tagged shrimp in unculled catches may be influenced by size of tagged shrimp relative to size of other shrimp in the catch and by overall volume of catch being processed. In the fall shrimping season (15 August–15 December), there are no restrictions on the amount of shrimp that can be retained. During 15 August–31 October, when white shrimp dominate the catch, the minimum shrimp count size is 50 (heads-on) per pound in major Texas bays (State of Texas 1987–88). Thus, commercial fishermen selectively retain larger shrimp during this interval. Since the TPWD gear used to collect white shrimp for tagging was relatively nonselective, surreptitiously-placed shrimp in Aransas Bay were smaller than those in the catch in which they were placed. In contrast, brown shrimp dominated the catch in summer when there was no count size restriction, and thus placed shrimp were similar in size to those in the commercial catch. Because the placed white

Table 1

Number and percent of tagged *Penaeus* shrimp surreptitiously placed on shrimp boat decks which were found and returned to TPWD.

Species	Bay system	No. tagged	Returned	
			n	%
P. aztecus (brown shrimp)	Galveston	43	6	14
	Aransas	72	18	25
	Total	115	24	21
P. setiferus (white shrimp)	Galveston	51	7	14
	Aransas	53	4	8
	Total	104	11	11
Combined species	Galveston	94	13	14
	Aransas	125	22	18
	Total	219	35	16

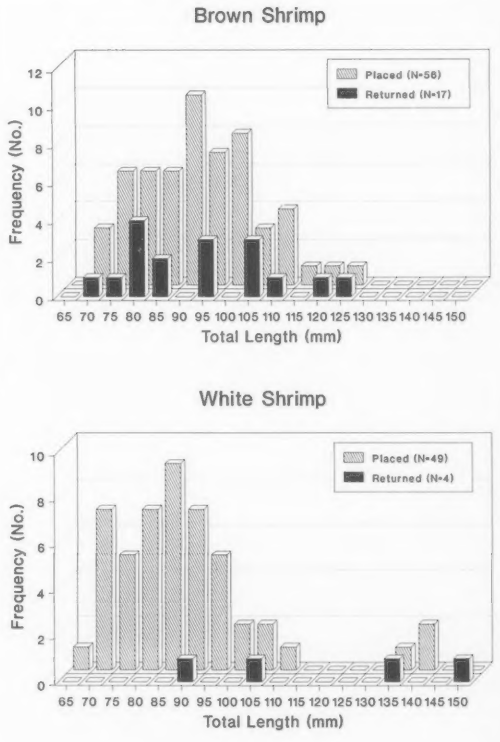
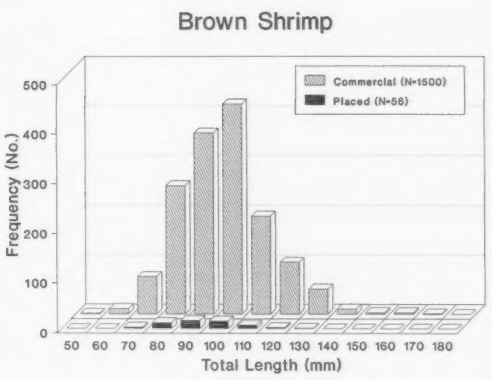


Figure 1

Length-frequency (TL) of surreptitiously-placed brown and white shrimp, and of returned brown and white shrimp from Aransas Bay, May–November 1984.



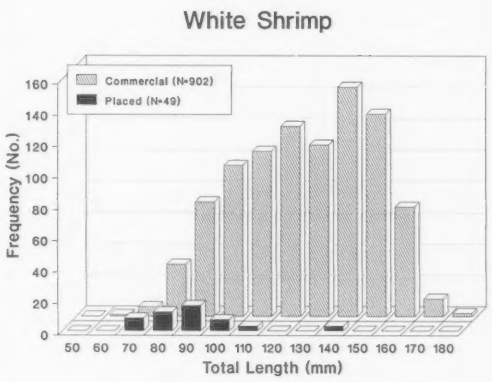


Figure 2

Length-frequency histograms of brown shrimp and white shrimp measured in commercial catches, and of tagged shrimp surreptitiously placed aboard boats in Aransas Bay, May–November 1984.

shrimp were smaller than those in the commercial catch, they may have been more difficult to detect and hence, were reported at a lower rate than if they had been similar in size to those in the commercial catch. The overall reporting rate with these white shrimp excluded was 19% (95% CI, 13–26%) which is similar to the reporting rate for brown shrimp (21%). Tagged and untagged brown shrimp sizes were similar.

Complete return of tags cannot be assumed even if rewards are offered. All tags used in the present study were potential reward tags ($50–500) inserted into the shrimp and placed into unculled shrimp catches; however, only 19% of these shrimp were reported. Past studies have relied on the use of monetary incentives to promote the return of tags. Rawstron (1971) determined that some reward tags in his fish-tagging study were not returned, but believed that this number was negligible. Likewise, Kutkuhn (1966) assumed low non-reporting rates for reward tags. Published estimates of tag-return rates for fish generally have ranged between 55 and 65%, with rewards. Green et al. (1983) reported much lower return rates by saltwater recreational anglers (29%) than had previously been estimated, and that rates differed among species and areas. Therefore, even with rewards, complete or high reporting rates cannot be assured.

Previous studies have relied on public-information dissemination plans to achieve high reporting rates of reward and non-reward tags. Matlock (1981) found that 83% (n 102) of the anglers not reporting tags in their catch knew about TPWD tagging programs, and that 78% of these anglers failed to find the tag. This suggests that public-information programs cannot assure high reporting rates. Even if fishermen are aware of tagging programs, they may not report recaptured tags if these programs have continued over a long period. The shrimp fishery in Texas had been subjected to frequent tagging experiments during the previous 10 years, and the shrimp fishermen's enthusiasm for reporting tags may have decreased. However, there are no data to examine this possibility.

Tag-return rates can be affected by many factors. Each tagging study that depends on volunteer tag returns would be enhanced by a concurrent estimate of non-reporting rates. This would improve estimates developed from returned tags. For example, during the tagging program conducted during the same period as this study, there were 2% of 25,870 released tagged shrimp returned (Peng Chai, TPWD, Austin, pers. commun.). If the reporting rate had been assumed to be 100% rather than the observed 19%, fishing mortality would be overestimated about five times.

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Power to detect linear trends in dolphin abundance: Estimates from tuna-vessel observer data, 1975-89

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Trends in abundance of dolphin stocks affected by the tuna purse-seine fishery in the eastern tropical Pacific Ocean (ETP) are of intense interest to a number of organizations concerned about the stocks' continued survival (Hammond and Laake 1983, Gerrodette 1987, Holt et al. 1987, Buckland and Anganuzzi 1988, Anganuzzi and Buckland 1989, Anganuzzi et al. 1991). The most straightforward method for estimating such trends is linear-regression analysis of relative abundance indices across time (e.g., Anganuzzi and Buckland 1989). Such abundance indices can be derived from data collected by observers aboard the tuna vessels (Buckland and Anganuzzi 1988, Anganuzzi and Buckland 1989, Anganuzzi et al. 1991). Linear trends in abundance over successive 5-year periods have been reported by Buckland and Anganuzzi (1988), Anganuzzi and Buckland (1989), and Anganuzzi et al. (1991).

Power analysis provides a method to quantify the probability of not detecting low rates of change in abundance over a specified time-period. It also provides a method, in cases where no statistically-significant trends are apparent, for determining the steepness of change necessary for its statistical detection given observed variability in the data, i.e., detectable trend (Gerrodette 1987, Peterman 1990). We use power analysis here to assess the efficacy of weighted linear-regression analysis for estimating linear trends in abundance of eight stocks of ETP dolphins. While it is instructive to evaluate the power of conclusions about observed trends, it is perhaps even more important to determine the magnitude of change required for detection of a trend, given observed variability in the dolphin abundance estimates. Therefore, we also calculate detectable trends, in addition to power of observed trends.

We present here estimates of observed trend, power to detect trends, and detectable trends for eight stocks of ETP dolphins, over time-series of 5, 8, and 10-years, assuming a two-sided hypothesis with $\alpha = 0.10$, using the noncentral t-distribution for the alternative hypothesis. Detectable trends were estimated assuming Type I (α) and Type II (β) error levels equal 0.10. We estimated power and detectable trends for all three sets of time-series to determine how much improvement might be expected by increasing the number of years included in the trend estimate. We did not include longer time-series, as it is unlikely that even a population with reproductive and individual growth rates as relatively slow as ETP dolphins would follow a linear trend for more than a decade, if that long.

Methods

Relative abundance indices and their associated bootstrap standard errors for eight stocks of ETP dolphins during the years 1975–89 (Table 1, Fig. 1) formed the database for the regression analyses presented here. Indices and standard errors for 1975–87 were taken from Anganuzzi and Buckland (1989), and for 1988 and 1989, from Anganuzzi et al. (1991). The eight dolphin stocks included northern offshore and southern offshore stocks of the pantropical spotted dolphin *Stenella attenuata*, the eastern spinner dolphin *Stenella longirostris orientalis*, northern and southern stocks of whitebelly spinner dolphin (hybrid/intergrades between *Stenella l. orientalis* and *Stenella l. longirostris* [Perrin 1990]), and northern, central and southern stocks of the common dolphin *Delphinus delphis*.

Observed trends

We estimated linear trends in relative abundance for each of the eight stocks over sequential series of 5, 8, and 10 years, using standard weighted least-squares regression (Wilkinson 1989). The slope of the regression (b) estimates the trend in abundance. The estimated standard error of the estimated trend (s_b) indicates the variability associated with the trend estimate. Weights were the reciprocal of the square of the bootstrap standard errors (Buckland and Anganuzzi 1988). We eliminated the estimate for 1983 from all analyses, because the presence of a very strong El Niño that year caused biologically unreasonable estimates of abundance for many of the stocks, in particular for northern offshore spotted dolphins, the stock affected by the fishery in greatest numbers (Buckland and Anganuzzi 1988, Anganuzzi et al. 1991). In the absence of any objective criteria for choosing which stocks were (or were not) affected by the El Niño, we elected to treat

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Table 1

Estimated abundances (first row) and bootstrapped standard errors (second row) for eight stocks of dolphins affected by the tuna purse-seine fishery in the eastern tropical Pacific Ocean. Values are in thousands. Data for 1975–87 from Buckland and Anganuzzi 1988; data for 1988–89 from Anganuzzi and Buckland 1989. Dashes indicate no values reported for that year. Asterisks indicate values from 1983 omitted as anomalous. SOPS boundaries (Anganuzzi and Buckland 1989) used in estimating southern offshore spotted dolphins. See text for scientific names.

	Dolphin stocks							
	1	2	3	4	5	6	7	8
1975	3949	—	599	490	—	122	404	385
	996	—	197	181	—	51	138	227
1976	4253	574	535	1205	115	344	287	586
	908	212	190	293	62	130	80	223
1977	3828	924	514	588	203	637	466	229
	751	332	152	163	87	200	90	162
1978	3212	584	395	613	65	358	329	—
	543	302	124	150	47	126	105	—
1979	2950	1040	428	366	—	650	644	—
	559	394	202	183	—	248	287	—
1980	3335	260	447	342	124	512	251	230
	582	168	112	99	86	191	85	139
1981	2536	199	255	694	124	513	111	435
	443	83	165	287	80	330	35	142
1982	2550	591	202	416	100	—	232	103
	557	180	91	132	47	—	101	90
1983	*	*	*	*	*	*	*	*
	*	*	*	*	*	*	*	*
1984	2158	244	340	253	182	—	71	—
	362	115	85	72	71	—	91	—
1985	2884	238	586	648	247	—	265	249
	352	68	124	128	64	—	105	318
1986	3165	154	584	451	—	475	169	—
	302	60	108	95	—	237	50	—
1987	2953	—	384	650	—	304	60	—
	293	—	87	105	—	123	18	—
1988	2689	79	717	484	88	323	241	253
	326	30	110	92	33	93	50	100
1989	2910	560	389	515	190	243	125	179
	275	140	71	78	69	107	24	47

1 = northern offshore spotted dolphin
2 = southern offshore spotted dolphin
3 = eastern spinner dolphin
4 = northern whitebelly spinner dolphin
5 = southern whitebelly spinner dolphin
6 = northern common dolphin
7 = central common dolphin
8 = southern common dolphin

all eight stocks similarly by eliminating the 1983 estimate.

For each series, we calculated regressions using as many data points as existed for each species for that number of years. In some cases, this resulted in as few as three data points contributing to the regression. Because we omitted data from 1983, the 10-year series contained at most nine data points. Because some years were omitted or were missing abundance indices, not all year-series comprised strictly consecutive x-values (year values).

We reexpressed the slope estimate of trend (b) in terms of a change parameter r, where

$$r = b/A_1$$

and A_1 (estimated abundance in first year of series) is calculated from the estimated slope and intercept for each year-series. For these linear regressions, the parameter r expresses the annual rate of change as a fraction of the estimated initial abundance (Gerrodette 1987). Linear regressions were calculated only for series with at least three data points.

Power

We estimated power of statistical conclusions about the significance of each slope by assuming a two-sided alternative hypothesis and using the non-central t (nct) distribution. In all cases, we assumed error levels $\alpha = \beta = 0.10$. We used a two-sided hypothesis test to be consistent with earlier estimates of 5-year trends in abundance (Buckland and Anganuzzi 1988, Anganuzzi and Buckland 1989, Anganuzzi et al. 1991).

To calculate power using the nct distribution, we utilized a series of programs (available upon request) designed to return power estimates as a function of three input variables:

$t_{\alpha,df}$ = normal t statistic given a level of α and degrees of freedom,

IDF = degrees of freedom, and

$\delta = b/s_b$.

Degrees of freedom were $n-2$ where n is the number of years for which abundance estimates existed in a series. Values for b and s_b were calculated from the weighted linear regressions.

δ is the offset of the alternative distribution (the nct) standardized by the standard error of the offset. In all cases, we assumed as the alternative distribution the observed trend for a series. δ is thus the distance, expressed as standard deviation units, between the mean of the null distribution (taken here to be zero slope) and the mean of the alternative distribution (the slope estimated from regression of the data).

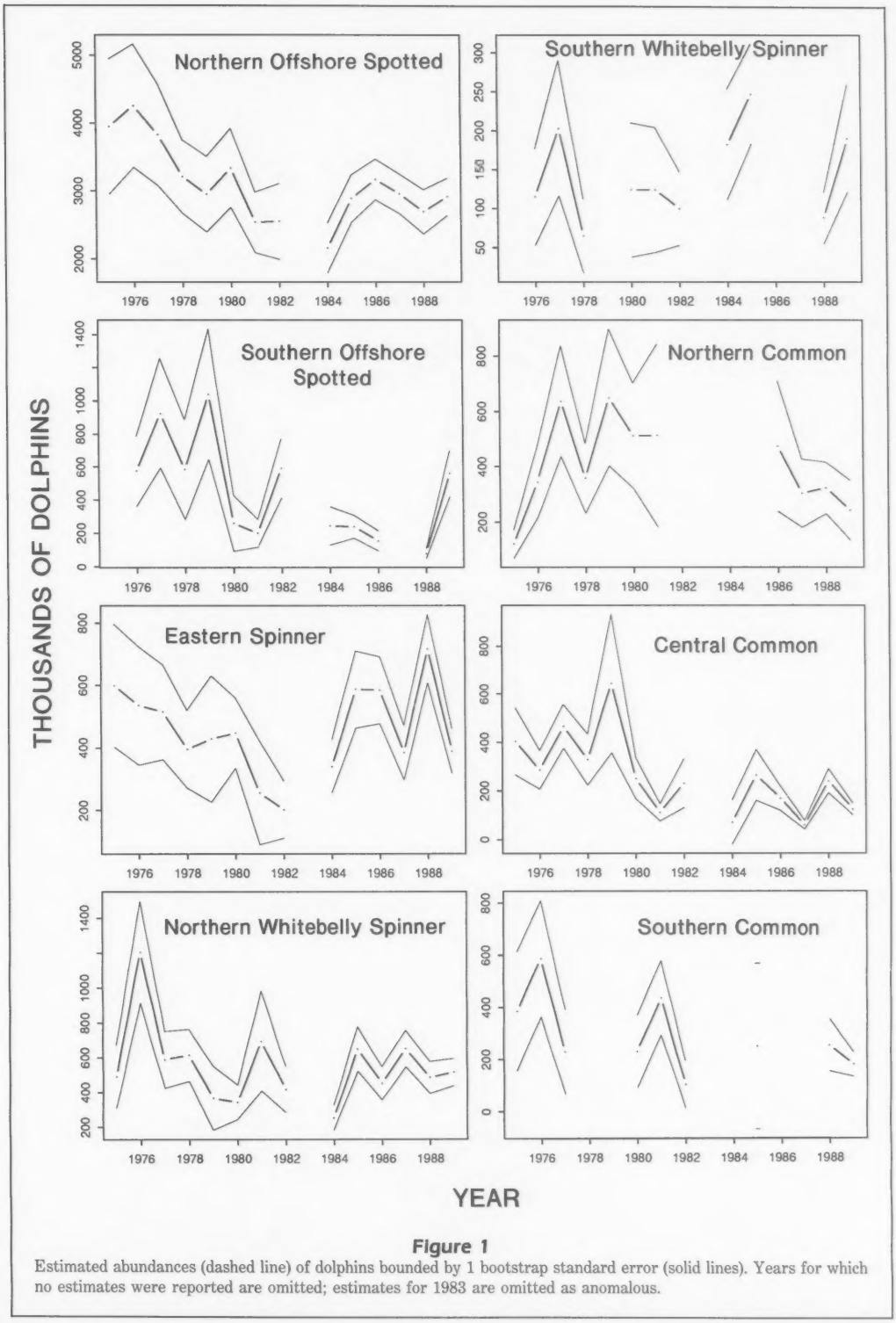

Figure 1

Estimated abundances (dashed line) of dolphins bounded by 1 bootstrap standard error (solid lines). Years for which no estimates were reported are omitted; estimates for 1983 are omitted as anomalous.

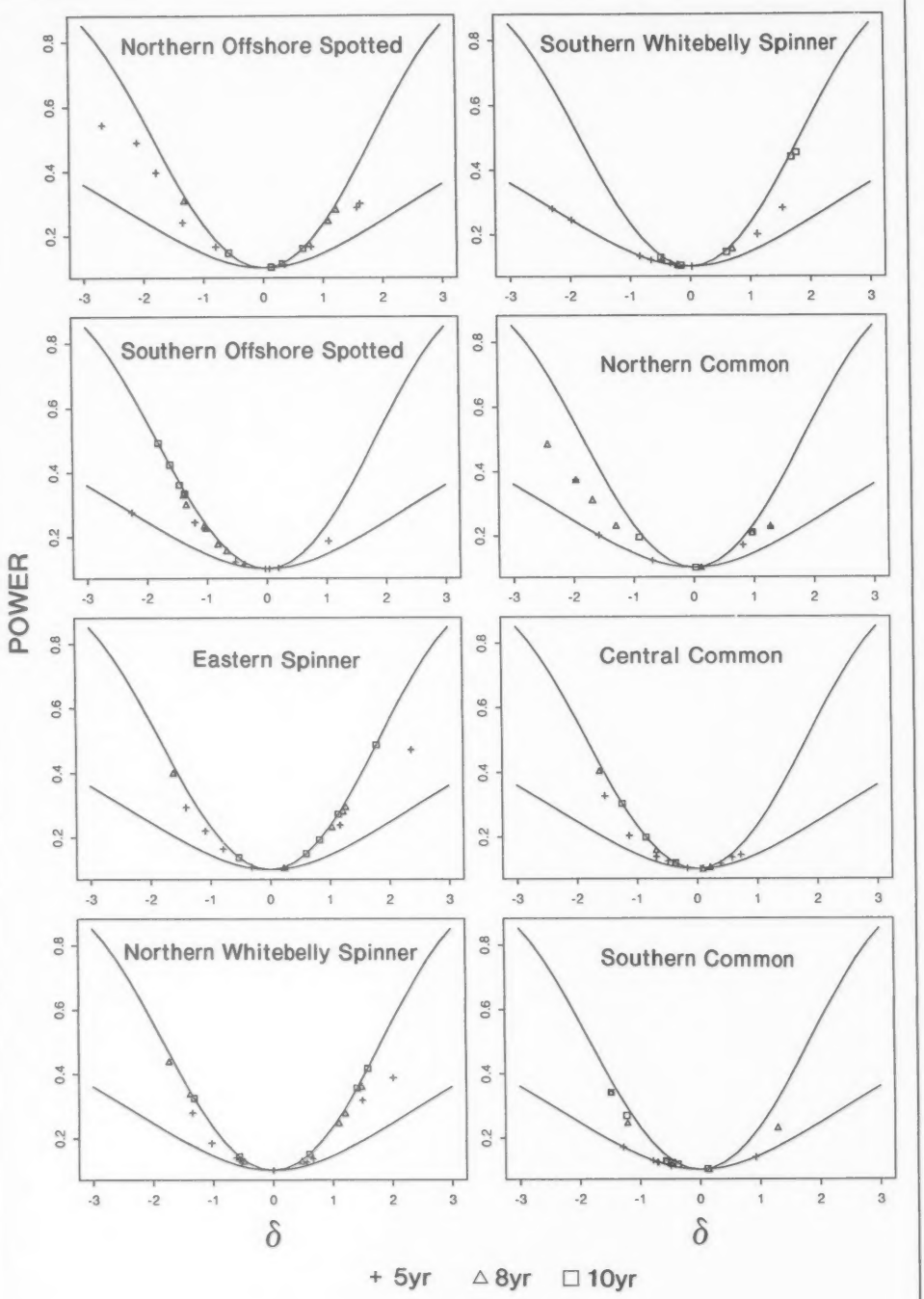

Figure 2

Power of conclusions about lack of statistical significance for estimated 5, 8, and 10-year trends in dolphin abundance. Power calculated for two-tailed noncentral t, assuming $\alpha = 0.10$. Solid lines indicate maximum (7 df) and minimum (1 df) power envelope. δ is the noncentral t parameter.

Detectable trends

We estimated detectable trends (r_d) for all data-series. All estimates of r_d assume error levels $\alpha=\beta=0.10$. Detectable trends were estimated by determining the value of Delta ($\delta_{0.9}$) that returns a power value of 0.90 from the nct algorithm. As before, input value for IDF was $n-2$, and for s_b was the value estimated from the weighted regression. Then the value of b generating the desired power level (b_{nct}) is

$$b_{nct} = \delta_{0.9}/s_b$$

and the detectable initial trend per year is

$$r_d = b_{nct}/A_1.$$

Results

Observed trends

The majority (151/192; 79%) of the series showed no significant trend (specific data available from the authors). Of those that did, most showed decreases prior to the mid-1980s and no consistent trends since. Where population-abundance indices changed relatively regularly over time, successively longer time-series retained the same general patterns as found in shorter series. For example, observed trends were significantly negative for northern offshore spotted dolphin during the 5-year series 75/79 and 77/81, the 8-year series 75/83, 76/83, and 77/84, and the 10-year series 75/84 and 76/85. Similarly, 5-year negative trends were also reflected in 8- and 10-year series for southern offshore spotted dolphin, eastern spinner dolphin, northern whitebelly spinner dolphin, and central common dolphin.

Data were so sparse and variable for southern whitebelly spinner dolphin and southern common dolphin that little can be said about trends in these stocks. Northern common dolphin were the only species for which trends may have switched during the period of investigation (from negative during earlier years, to positive more recently); but it is obvious that here, as in the other series, the pattern in trend estimates is simply a function of the length of the series selected and its placement in time.

Power

Power to reject a false null hypothesis increases with increases in either or both of series length (as degrees of freedom increase) or δ (offset) (Fig. 2), but for TVOD the increases generally were not sufficient to be of practical use. Where no significant trends (slopes) were found, power to detect a false null hypothesis was low, averaging 20–30% in most cases and never exceeding 60%. Power for each test was small because the alternative hypothesis for these power calculations was taken to be the observed slope, which was usually fairly small, and also because scatter around the regression line tended to be large. Therefore the null and alternative distributions overlapped considerably. The low power of these tests simply means that if the true slope equaled the observed slope, the power to distinguish the true slope from a slope of zero (i.e., no change in abundance) would be quite small in most cases.

Detectable trends

The range of detectable trends decreased rapidly with increasing series-length in all cases (Fig. 3), as this increases the degrees of freedom (number of data points). The decrease is misleading in most cases, however. Although the improvement in ability to detect smaller trends with longer time-series appears dramatic, in most cases even the smallest detectable trends are still much too large to be of use.

Even with as many as 10 years of data in a series, linear trends less than about 10% per year could be detected consistently only for northern offshore spotted dolphin. For all other stocks, trends of at least 15–20% per year would be required to produce a significant result (Fig. 2). Series lengths would have to be such that populations more than doubled or decreased to zero in order for the change to be statistically detectable. This would require series lengths of at least 10 years.

In many cases, where significant trends were found, these trends were of lesser magnitude than the estimated detectable trend. This occurs because the estimated detectable trend is the expected value of the alternative distribution. Any trend value which falls below this expected value, but which also falls above the Type-I error limit for the null distribution, will be assumed significantly different from the null even though the trend could actually belong to either distribution. For example, if the Type-I error limit for the null distribution occurs at a trend value of 0.75 (i.e., if the cut-off point for values assumed to belong to the null distribution is 0.75), and the expected value (i.e., the mean) for the alternative distribution falls at 0.85, any trend value within the range 0.75–0.85 will be assigned to the alternative distribution even though it is smaller than the expected value of the alternative distribution. In practice for the ETP data, this effect is unimportant compared with the overall problem of high variability obscuring the possibility of detecting managerially-relevant trends in abundance (i.e., the

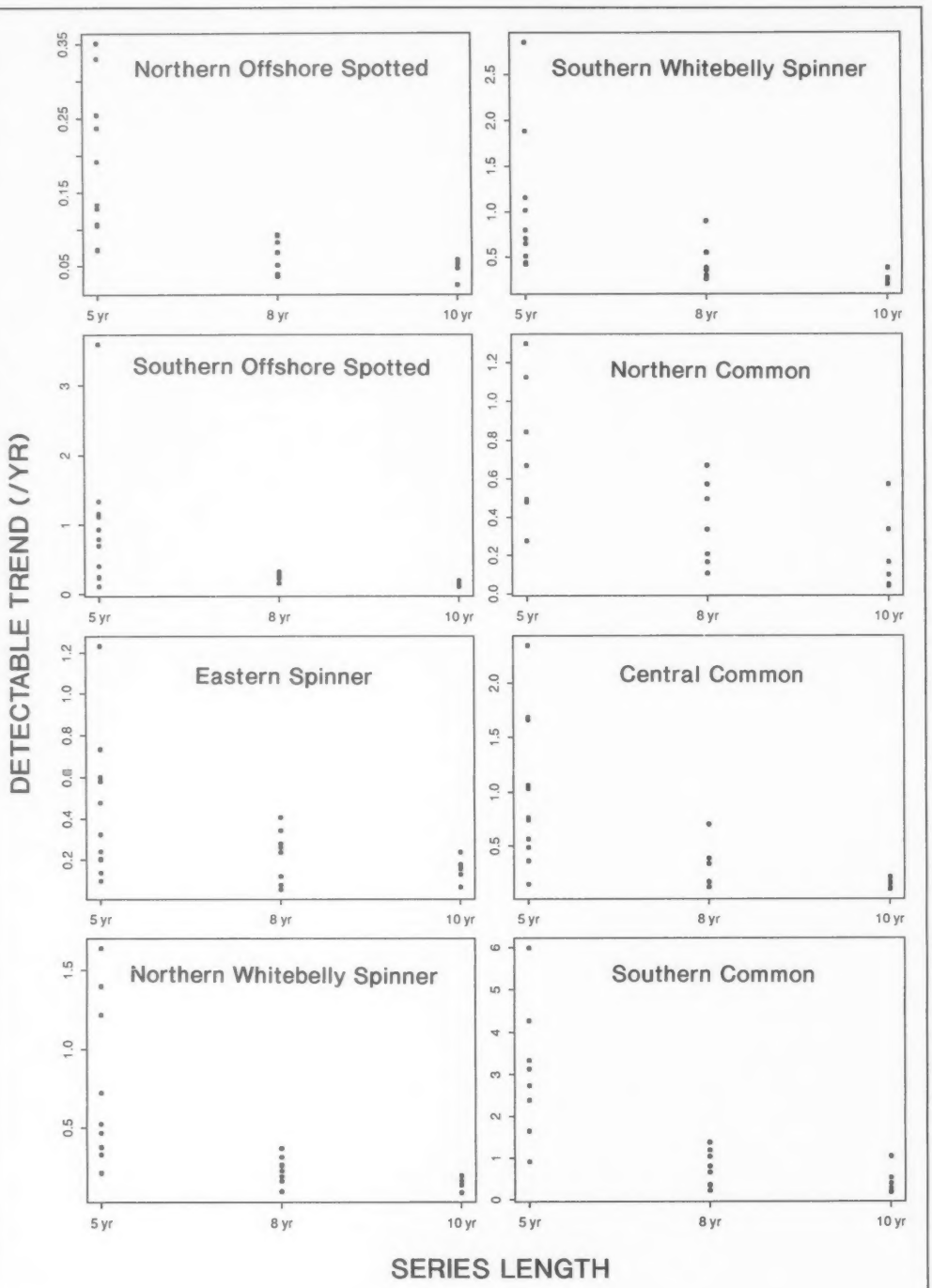

Figure 3
Estimated detectable trends for successive 5, 8, and 10-year series of tuna vessel observer data.

spread and subsequent overlap between null and alternative distributions is so great that differences between the cut-off point in the null and the mean of the alternative is effectively inconsequential).

Discussion

Given the observed variability in TVOD, it does not appear that linear trends in dolphin abundance estimated from these data with these techniques will be detectable at any levels practical for management purposes, except possibly for the stock of northern spotted dolphin. Even for this stock, survey series at least a decade in length are required.

Our estimates of 5-year trends agree with previously published estimates derived by the same methods, where 1983 has been omitted from the analyses (Anganuzzi and Buckland 1989). Our results imply that for time-periods as short as 5 years, considerably larger trends than those observed would be necessary to produce estimates of significant change with any reasonable power. Except for northern offshore spotted dolphin, this applies also to all other stocks, even for the maximum time-series tested (10 years in this study). It appears that other methods must be found to determine whether trends truly exist in dolphin abundance in the ETP. For management purposes, longer time-series must be monitored, for which linearity cannot be assumed. Other regression procedures making greater use of the precision estimates (standard errors) of the indices could have more power, but for linear analyses, at least, it is uncertain whether the increase in power could overcome the inherent variability and probable nonlinearities in the data.

A more effective approach to estimating trends in dolphin abundance is probably represented by the sophisticated smoothing method applied recently to these data by Buckland et al. (1992). The method reduces the relatively-scattered abundance estimates to smoothly-changing estimates of abundance, but with the advantage of producing confidence limits about the smoothed trend and generating a more biologically-reasonable result (abundance of natural populations rarely changes linearly). However, simulation experiments will be required to determine the circumstances under which the smoothed trends do, or do not, reflect accurately the true underlying dynamics of the stocks. Such simulations are currently underway, but results are as yet unavailable (Alejandro Anganuzzi, Inter-Am. Trop. Tuna Comm., La Jolla, pers. commun., July 1991).

Regardless of the results of the tests of various smoothing methods, it appears fruitless, based on the results presented here, to use linear-regression techniques to estimate trends in abundance of dolphin stocks in the ETP, even for periods as long as a decade. The power to detect ecologically (or managerially) relevant trends, given the observed variability in the data, is simply not sufficient.

Future efforts should, as suggested by Buckland et al. (1992), focus on developing or applying robust, curvilinear smoothing techniques that are reasonably responsive to the underlying processes or mechanisms controlling actual changes in dolphin abundance.

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